Edited by
W.A. Montevecchi and A.J. Gaston

Studies of high-latitude seabirds. 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology

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Northern Fulmar in Davis Strait
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Introduction

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Seabirds are the most wide-ranging and visible upper-trophic-level consumers in marine ecosystems. The ease with which birds can be observed and monitored, their tendencies to aggregate in areas of high production, their interactions at different trophic levels, and their sensitivities and vulnerabilities to environmental perturbation and degradation combine to make them excellent natural indicators of prey availability and of the general health of the marine environment. In addition, seabirds attract public attention. When eggs fail to hatch at spectacular coastal seabird colonies because of pesticide contamination or when seabirds die from oiling and their corpses wash up on beaches — events that are pervasive signals of marine pollution — people react.

Much recent research effort has been directed at seabird feeding ecology, which is central to many multi-disciplinary studies of marine foods webs (e.g., Nettleship et al. 1984; Croxall 1987; Furness and Monaghan 1987; Vermeer and Butler 1989). The present collection, an outgrowth of a symposium held at Memorial University of Newfoundland in April 1989 and jointly sponsored by the Ocean Sciences Centre and the Canadian Wildlife Service, includes behavioural, energetic, and oceanographic aspects of seabird feeding ecology. The papers represent a cross section of marine ornithology focused on the ecology of birds at sea.

The object of the symposium held at Memorial University of Newfoundland was to bring together researchers and conservationists to present some current issues in marine ornithology and to explore ways in which science can illuminate and enhance conservation biology. Two of the papers included here illustrate ways in which technological advances have allowed us to study previously hidden aspects of avian ecology — diving depths (Burger) and trophic levels (Hobson). Schneider and Bajdik's contribution demonstrates how the application of a rigorous statistical approach can improve the value of counts of birds made at sea, an important aspect of monitoring and environmental assessment studies. The other papers (Piatt et al., Springer, and Brown) deal with relationships between marine bird distributions and biological and physical oceanographic processes that influence them. It is necessary to understand these biophysical interactions in order to be better able to differentiate natural from human-induced perturbation in marine ecosystems.

The symposium occurred at a time when traditional fisheries off eastern Canada were severely depressed. An intense debate was, and still is, in progress over the possible causes of declines in major fish stocks (Harris 1990). These problems have intensified and have involved fish plant closures and consequent social and economic disruptions. Changes in fish stocks, whatever their cause, are not without consequences for marine birds, which are predators of, or potential competitors with, many fish species. Predicting interactive effects within multispecies food webs is a difficult and important course of research investigation; the papers by Hobson, Piatt et al., and Springer contribute to this process.

A major event with potentially extremely important consequences for marine birds over the whole of the North Atlantic occurred since the meeting at Memorial University of Newfoundland. In September 1990, the governments of Canada and Newfoundland and Labrador decided to proceed with the development of the Hibernia oil field on the Grand Bank. This multibillion-dollar project proposes to place oil terminals 300 km from shore in relatively deep water, regularly traversed by icebergs. The Grand Bank, one of the richest fishing grounds in the world, is very important at all times of year for large populations of marine birds and mammals. The seabirds include millions of breeding birds from the large colonies in Newfoundland and Labrador, nonbreeding transients from the southern hemisphere and Europe, as well as winter visitors from the eastern Canadian Arctic, Greenland, Iceland, and as far afield as Svalbard.

Much money and effort have been expended on attempting to assess the possible impacts of the Hibernia development on marine ecosystems and to design the safest possible technology. The human and ecological dangers are, however, very real. The Ocean Ranger drilling rig, lost in a winter storm in 1982 with all crew on board in the Hibernia area, cannot be forgotten. The Hibernia development, which includes a shore terminal in Trinity Bay, close to the massive seabird colonies on Baccalieu and Funk islands, will have many impacts on marine birds; some have the potential to be devastating. Baccalieu Island, which is home to the largest species diversity and largest population of breeding seabirds in all of eastern Canada (Montevecchi and Tuck 1987; Sklepkovych and Montevecchi 1989), has yet to be recognized by either the provincial or federal governments as an ecological reserve! The seabird colony of Baccalieu is of international biological significance and as such garners more interest from foreign scientists than it has from local governmental agencies.

Hydrocarbons illegally and legally discharged into the offshore and inshore waters of the northwest Atlantic

have long been known to take large tolls of seabirds, especially in winter (Tuck 1959). The reactivation of the oil refinery at Come by Chance at the head of Placentia Bay and the associated increase in tanker traffic have aggravated the situation. The Government of Canada has undertaken a commission to study tanker safety and oil pollution at sea, yet there are no bilge flushing facilities in any ports in Newfoundland and Labrador. Accidental spills at sea are a very significant issue to be addressed and are no doubt inevitable as the Hibernia project progresses. However, most of the oil pollution at sea is not accidental but deliberate and preventable. Marine ornithological research will greatly aid in defining the dimensions of these problems and in designing solutions that will protect birds, the natural indicators of the ocean's renewable resources upon which our long-term wealth and health depend. The Canadian Wildlife Service, the Ocean Sciences Centre, and local, regional, national, and international conservation groups will be actively involved in studying the biological effects of hydrocarbon exploitation.

This Occasional Paper is the first of three to be focused on research on high-latitude seabirds. A forthcoming volume will deal with the population dynamics of Thick-billed Murres *Uria lomvia*. A large-scale energetics model, which estimates the spatial and temporal prey harvests of seabirds throughout the year, was also presented during the symposium and will be published as a subsequent contribution in this series. As our understanding of avian trophic interactions and their behavioural, energetic, and oceanographic involvements improves, so will our ability to identify and protect critical marine resources and habitat. It is our ocean, and it is up to all of us to protect it.

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Maximum diving depths and underwater foraging in alcids and penguins

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Abstract

Maximum diving depths (d_{max}, in m) attained by alcids and penguins varied allometrically with body mass (M, in kg) as follows: $d_{max} = 75.905\ M^{0.316}$ ($r^2 = 0.522$, $n = 19$). The diving depths reached by alcids were similar to or deeper than those of penguins, relative to body mass, even though alcids are generally regarded as being less well adapted for diving than penguins. It is not known whether these birds achieved the deepest dives using only aerobic metabolism, but an oxycalorific model predicts that this was unlikely. Models of foraging efficiency indicated that anaerobic dives in the Common Murre *Uria aalge* could be profitable, despite long recovery times, and might be undertaken by birds taking abundant deep-water prey. A review of data from time-at-depth recorders indicated that penguins and alcids spent most time foraging at depths much shallower than the maximum possible, and probably within aerobic depth limits.

Résumé

On a déterminé que les profondeurs maximales de plongée (d_{max}, en m) atteintes par les alcidés et les manchots varient de façon allométrique en fonction de la masse corporelle (M, en kg) suivant l'équation suivante : $d_{max} = 75{,}905\ M^{0.316}$ ($r^2 = 0{,}522$, $n = 19$). Les alcidés atteignent des profondeurs égales et plus grandes que les manchots, compte tenu de leur masse corporelle, en dépit du fait qu'ils sont généralement considérés comme moins bien adaptés à la plongée que ces derniers. On ignore si les plongées faites aux profondeurs maximales sont en métabolisme aérobie seulement, mais ce serait peu probable d'après un modèle oxycalorifique. Selon des modèles de l'efficacité d'alimentation, les plongées anaérobies pourraient être profitables aux Marmettes de Troïl *Uria aalge*, malgré les longues durées de récupération, et elles pourraient être effectuées par des oiseaux capturant une abondance de proies en eau profonde. Des enregistrements du temps passé à diverses profondeurs indiquent que les manchots et les alcidés passent la plus grande partie du temps à chercher leurs proies à des profondeurs beaucoup plus faibles que le maximum possible, et probablement à des profondeurs inférieures aux limites des plongées aérobies.

1. Introduction

The physiological constraints of breath-hold diving are important in shaping the behaviour and foraging niches of diving seabirds. This fact has been recognized for over a century (Butler and Stephenson 1987), but, until recently, there has been little integration of laboratory-based physiology and field-oriented ecology. In the past, physiologists often used inappropriate species (e.g., dabbling ducks) and worked under highly artificial conditions, with the result that their data were of little value to ecologists (see reviews by Butler and Jones 1982; Butler and Stephenson 1987; Jones and Furilla 1987). Ecologists, on the other hand, faced with logistical problems in studying free-living diving birds at sea, could make very limited, and sometimes incorrect, assumptions about the birds' use of the water column (e.g., Ashmole 1971; Cody 1973).

Since the late 1970s, major advances have been made in the study of the physiological ecology of diving seabirds, facilitated by the use of doubly labelled water, radio-telemetry, and miniaturized gauges to record heart rates, swimming speeds, diving depths, and time budgets at sea (e.g., Butler and Woakes 1984; Nagy et al. 1984; Wilson 1985; Cairns et al. 1990). Detailed observations of the activities and dive durations at various depths are necessary for a better understanding of underwater foraging ecology. Records of maximum diving depths, which can be obtained cheaply and accurately (Burger and Wilson 1988), can also provide useful information on the limits of a bird's dives and its access to deep prey (Piatt and Nettleship 1985; Burger and Simpson 1986).

This paper reviews diving depths of alcids and penguins. These seabirds utilize wing-propelled underwater "flight" and are the dominant seabirds of the cool-temperate and polar regions. There are few reliable depth records for other important diving seabirds, such as cormorants and diving-petrels. Major considerations in the paper include:

(1) derivation of allometric equations for maximum diving depths;
(2) development of speculative models to explore whether these deep dives might be attained by solely aerobic metabolism;
(3) investigation of foraging efficiency associated with various diving regimes; and
(4) comparisons of maximum diving depths with results from time-at-depth recorders.

Table 1
Maximum diving depths recorded for free-living seabirds[a]

Species	Mass (kg)	Max. depth (m)	Method[c]	Sample size	Reference
Penguins					
Emperor *Aptenodytes forsteri* (ep)	22.0	265[b]	MDG	5 birds	Kooyman et al. 1971
King *A. patagonicus* (kp)	13.0	240[b]	TDR	2595 dives by 3 birds	Kooyman et al. 1982
Gentoo *Pygoscelis papua* (gp)	5.5	100	NET	1 bird	Conroy and Twelves 1972
Gentoo	5.5	70	MDG	19 birds	Adams and Brown 1983
Gentoo	5.5	135[b]	TDR	1444 dives by 14 birds	Croxall et al. 1988
Gentoo	5.5	136	TDR	10 birds	Wilson 1989
Chinstrap *P. antarctica* (cp)	3.5	70[b]	TDR	1110 dives by 4 birds	Lishman and Croxall 1983
Adelie *P. adeliae* (ap)	5.0	80[b]	TDR	20 birds	Wilson 1989
Macaroni *Eudyptes chrysolophus* (mp)	4.6	110[b]	TDR	6352 dives by 8 birds	Croxall et al. 1988
Jackass *Spheniscus demersus* (jp)	3.2	130[b]	MDG	15 birds	Wilson 1985
Magellanic *S. magellanicus* (mag)	3.5	73[b]	MDG	NR	Wilson and Wilson 1990
Humboldt *S. humboldti* (hp)	4.2	80[b]	MDG	NR	Wilson and Wilson 1990
Little *Eudyptula minor* (lp)	1.2	69[b]	MDG	32 birds	Montague 1985
Alcids					
Common Murre *Uria aalge* (cm)	0.93	180[b]	NET	12 243 birds	Piatt and Nettleship 1985
Common Murre	0.93	138	MDG	2 birds	Burger and Simpson 1986
Thick-billed Murre *U. lomvia* (tm)	0.92	153[b]	MDG/TDR	24 birds	AEB, unpubl. data
Razorbill *Alca torda* (ra)	0.74	120	NET	11 birds	Piatt and Nettleship 1985
Razorbill	0.74	140[b]	SUB	1 bird	Jury 1986
Atlantic Puffin *Fratercula arctica* (apu)	0.51	60	NET	875 birds	Piatt and Nettleship 1985
Atlantic Puffin	0.51	68[b]	MDG	8 birds	Burger and Simpson 1986
Rhinoceros Auklet *Cerorhinca monocerata* (ra)	0.52	63[b]	MDG/TDR	15 birds	AEB, unpubl. data
Black Guillemot *Cepphus grylle* (bg)	0.43	50[b]	NET	36 birds	Piatt and Nettleship 1985
Pigeon Guillemot *C. columba* (pg)	0.45	30[b]	MDG	2 birds	AEB, unpubl. data
Cassin's Auklet *Ptychoramphus aleuticus* (ca)	0.19	30	ECHO	—	Dolphin and McSweeney 1983
Cassin's Auklet	0.19	43[b]	MDG/TDR	23 birds	Burger and Powell 1990
Dovekie *Alle alle* (do)	0.16	35[b]	NR	—	Prince and Harris 1988
Cormorants					
Cape *Phalacrocorax capensis*	1.20	92	MDG	7 birds	R.P. Wilson, unpubl. data
Bank *P. neglectus*	1.95	70	MDG	2 birds	R.P. Wilson, unpubl. data
Crowned *P. coronatus*	0.76	11	MDG	2 birds	R.P. Wilson, unpubl. data
Blue-eyed *P. atriceps*	2.20	125	MDG	NR	S. Wanless, unpubl. data
Shag *P. aristotelis*	1.70	43	MDG/TDR	39 birds	Wanless et al. 1991
Shag	1.70	80	NET	NR	Guyot 1988

[a] Abbreviations of species used in Figure 1 are given in parentheses.
[b] These depth values were used in the regressions.
[c] Methods used: maximum depth gauge (MDG); birds caught in fishing net (NET); time-at-depth recorder (TDR); eaten by a whale seen feeding on euphausiids seen on echosounder (ECHO); seen from a submersible (SUB); not reported (NR).

2. Materials and methods

Much of this paper is based upon reviews of published material. The depths of the sea in which the birds foraged and the depths at which their prey aggregated were seldom reported, and therefore no attempt was made to correlate maximum diving depths with these parameters. Depths recorded for birds caught in nets and traps are sometimes unreliable (Kooyman and Davis 1987) and have been used only when supported by additional measurements. For example, the maximum depths reported for four alcids caught in nets off Newfoundland (Piatt and Nettleship 1985) correspond with measurements made with gauges on two of these species in the same area (Burger and Simpson 1986) and with observations made from a submersible on a third species (Jury 1986).

New data are given on diving depths for the following species: Thick-billed Murres *Uria lomvia* at Coats Island, N.W.T., in August 1987 and 1988; Rhinoceros Auklets *Cerorhinca monocerata* at Triangle Island, B.C., in July 1986; and Pigeon Guillemots *Cepphus columba* at Seabird Rocks, Vancouver Island, B.C., in July 1986. All were breeding adults feeding chicks. Maximum diving depths were recorded using two gauges. Capillary-tube maximum depth gauges (MDGs) were constructed and deployed as described by Burger and Wilson (1988). Time-at-depth recorders (TDRs) were the type described by Wilson et al. (1989), in which the depth-dependent position of a light-emitting diode is recorded as an image on photographic film. The position and optical density of the image indicate the depth and the duration of time at each depth, respectively. Details on these studies will be published shortly.

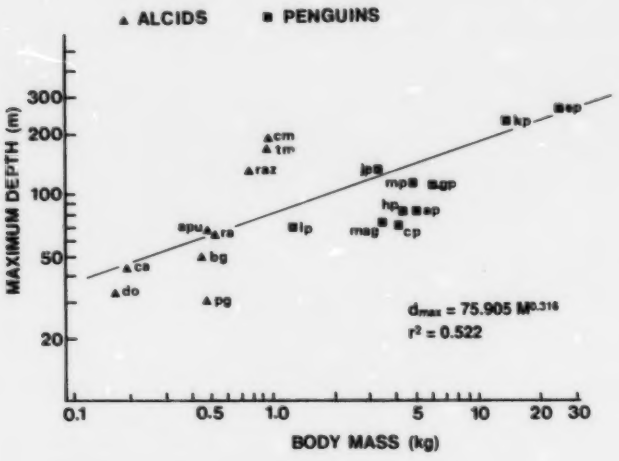
3. Results and discussion

3.1. Maximum diving depths

Maximum diving depths attained by 10 species of penguins and nine alcids are given in Table 1. When the deepest recorded depths of each species were compared with body mass, significant allometric relationships were found (Fig. 1, Table 2). The r^2 values of the regressions were higher when penguins and alcids were treated separately than when combined (Table 2). These equations suggest that alcids can dive considerably deeper than penguins, relative to their body mass. The alcid equation is, however, strongly affected by the exceptional depths recorded for the two murres and the Razorbill *Alca torda* (Fig. 1), and it predicts that the Great Auk *Pinguinis impennis* (mass at least 5.5 kg) (Bédard 1985) could have reached a depth of 570 m! The penguin–alcid equation, on the other hand, predicts a maximum depth of 130 m for the Great Auk. Most alcids appear to fit the same depth–mass regression as penguins, and, until further data are available from a wider range of species, the parsimonious approach is to combine the penguin and alcid data (Fig. 1). The maximum depths (d_{max}, in m) attained by wing-propelled diving birds can thus be predicted from body mass (M, in kg) as follows:

$$d_{max} = 75.905\, M^{0.516} \quad (1)$$
$$(r^2 = 0.522,\ n = 19,\ P < 0.001)$$

Figure 1
Maximum diving depths measured in penguins and alcids. The regression line and equation show the relationship between maximum depths and body mass for alcids and penguins. See Table 1 for species abbreviations.



There is a fairly wide scatter of maximum depths about the regression line, indicating that factors other than body mass affect maximum depths. The distribution and type of prey are likely to be important but are difficult to assess with the available data, and no obvious trends can be seen. In general, species taking predominantly fish appear to be scattered from well above (e.g., murres and Razorbill) to well below (e.g., Pigeon Guillemot, Magellanic Penguin *Spheniscus magellanicus*) the regression line. Species relying on zooplankton fall close to or below the line (e.g., Cassin's Auklet *Ptychoramphus aleuticus*, Macaroni Penguin *Eudyptes chrysolophus*), but Thick-billed Murres, which fall well above the line, also take considerable quantities of zooplankton (Bradstreet and Brown 1985).

Maximum diving depths of five species of cormorant, obtained primarily from unpublished studies, are shown in Table 1 for comparison with alcids and penguins. The maximum depths of four of the five species fall within the cluster of those of penguins and alcids of similar body masses, but one species, the Crowned Cormorant *Phalacrocorax coronatus*, did not reach the anticipated depth. I tentatively conclude that the abilities of the foot-propelled cormorants to reach deep prey are similar to those of the wing-propelled penguins and alcids, but this topic obviously requires additional study.

3.2. Modeling maximum aerobic depths

In an attempt to determine whether the maximum depths measured were attainable using aerobic metabolism, as suggested by Kooyman and Davis (1987), a simple model was constructed. Birds of mass 13 kg (large penguin), 5 kg (medium-sized penguin), 1 kg (largest alcid), 0.5 kg (puffin-sized alcid), and 0.2 kg (small auklet) were compared. The model assumes that maximum depths (d_{max}) are attained during bounce-dives (Kooyman and Davis 1987), and hence depth is determined by velocity (V) and dive time (T_d):

$$d_{max} = 0.5\ V\ T_d \qquad (2)$$

Underwater velocity is difficult to estimate reliably and appears to increase with body mass in penguins (Kooyman and Davis 1987) but not in cormorants (Wilson and Wilson 1988). D.A. Croll (pers. commun.), using

Table 2
Relationships between maximum diving depths (d_{max}, in m) and body mass (M, in kg) for penguins and alcids

Group	Allometric equation	No. of species	r^2	P
Penguins	d_{max} = 48.990 $M^{0.321}$	10	0.713	<0.01
Alcids	d_{max} = 132.222 $M^{0.855}$	9	0.677	<0.01
Penguins and alcids	d_{max} = 75.905 $M^{0.316}$	19	0.522	<0.001

miniature pressure gauges, found that the rate of ascent and descent in murres averaged 1 $m \cdot s^{-1}$ but could reach 3 $m \cdot s^{-1}$. In this model, I assumed that the vertical velocities of deep dives were higher than average cruising or gliding speeds (see Kooyman and Davis 1987) and used velocities of 1.2, 1.3, 1.5, 1.8, and 2.0 $m \cdot s^{-1}$ for birds of mass 0.2, 0.5, 1, 5, and 13 kg, respectively.

Time spent underwater (T_d) with aerobic metabolism depends on the total oxygen stored in the bird's respiratory system, blood, and myoglobin (O_{store}) divided by the rate of oxidative metabolism (O_{use}), and hence maximum aerobic depths (d_{oxy}) can be calculated as:

$$d_{oxy} = 0.5\ V\ O_{store}/O_{use} \qquad (3)$$

Respiratory oxygen capacity varies with body mass as $M^{1.19}$ in domestic Mallards *Anas platyrhynchos* of various ages (Hudson and Jones 1986) and as $M^{0.91}$ in a series of bird species (Lasiewski and Calder 1971). Both are similar to isometric relationships (i.e., $M^{1.0}$). I therefore assumed that total oxygen stores scale isometrically at 44.5 mL $O_2 \cdot kg^{-1}$ (the mean of values given by Kooyman and Davis 1987). Keijer and Butler (1982) reported a similar value (41.5 mL $O_2 \cdot kg^{-1}$) for the Tufted Duck *Aythya fuligula*.

Oxygen consumption depends on metabolic rate, which varies with swimming speed (Woakes and Butler 1983; Baudinette and Gill 1985). As a first approximation, metabolic rates during dives were treated as mass-dependent variables in the model and calculated as multiples of the standard metabolic rates (SMR), derived from the daytime, nonpasserine allometric equation (4.41 $M^{0.729}$ $J \cdot s^{-1}$) (Aschoff and Pohl 1970). The SMR was converted using an oxycalorific equivalent (20.1×10^6 $J \cdot m^{-3}$ O_2) (Peters 1983:51) to give the resting oxygen consumption as 0.219 $M^{0.729}$ mL $O_2 \cdot s^{-1}$.

Calculations of this model are shown in Table 3. The resultant curves show how the predicted maximum aerobic depth limit will vary as the metabolic cost of diving increases (Fig. 2). The major finding here is that in order to attain the maximum depths predicted from the allometric equation (Eq. 1), the diving metabolism of the birds should not exceed 1.5–2 × SMR for small birds or 2–3 × SMR for large birds (Fig. 2). Could such depths be reached with these low metabolic outputs?

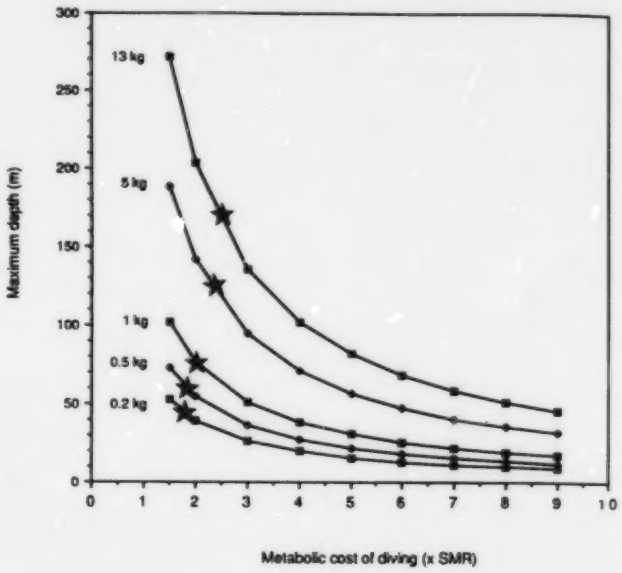
Measurements of the costs of underwater locomotion vary according to the method used. Laboratory studies using oxygen consumption gave estimates of underwater swimming of 2.1 times resting rates in Little Penguins *Eudyptula minor* (Baudinette and Gill 1985) and 1.26 times resting rates in Humboldt Penguins *Spheniscus humboldti* (Butler and Woakes 1984). However, because birds resting in water are not in a thermoneutral state, their metabolic rates should be 1.1–1.2 times higher than standard resting-in-air rates (Kooyman and Davis 1987) and higher still in cold water (Butler and Stephenson 1987). Diving metabolism measured with doubly labelled water using free-living Jackass Penguins *Spheniscus demersus* was 9.8 × SMR (Nagy et al. 1984). No estimates of diving costs of alcids appear to be available. Cairns et al. (1990) found

Table 3
Calculations of the model to predict maximum aerobic diving depths and dive times for penguins and alcids for metabolic costs of diving ranging between 1.5 and 9 × SMR, and assuming bounce-dives with no time foraging[a]

Parameter	Small auklet	Medium-sized alcid	Large alcid	Medium-sized penguin	Large penguin
(A) Body mass (kg)	0.2	0.5	1	5	13
(B) Resting metabolic O_2 use ($mL \cdot s^{-1}$)	0.068	0.132	0.219	0.708	1.421
(C) Oxygen store ($mL \cdot kg^{-1}$)	44.5	44.5	44.5	44.5	44.5
(D) Total oxygen store (mL) (A × C)	8.9	22.25	44.5	222.5	578.5
(E) Assumed velocity ($m \cdot s^{-1}$) (see text)	1.2	1.3	1.5	1.8	2.0
(F) Calculated maximum aerobic diving depth (m) with multiples of SMR[b]					
1.5	52.5	73.0	101.6	188.6	271.5
2	39.4	54.7	76.2	141.4	203.6
3	26.3	36.5	50.8	94.3	135.7
4	19.7	27.4	38.1	70.7	101.8
5	15.8	21.9	30.5	56.6	81.4
6	13.1	18.2	25.4	47.1	67.9
7	11.3	15.6	21.8	40.4	58.2
8	9.9	13.7	19.0	35.4	50.9
9	8.8	12.2	16.9	31.4	45.2
(G) Calculated maximum dive times (s) for dives from F Multiple of SMR:					
1.5	88	112	135	210	271
2	66	84	102	157	204
3	44	56	68	105	136
4	33	42	51	79	102
5	26	34	41	63	81
6	22	28	34	52	68
7	19	24	29	45	58
8	16	21	25	39	51
9	15	19	23	35	45

[a] See text for the source of the data.
[b] F calculated as: $\frac{0.5 \times \text{velocity (E)} \times \text{oxygen store (D)}}{\text{Resting } O_2 \text{ use (B)} \times \text{multiple of SMR}}$

Figure 2
Model predictions of the maximum depths attainable using aerobic metabolism for birds of mass 0.2–13 kg, with varying estimates of the metabolic costs of aerobic diving. See text and Table 3 for inputs and working of the model. The stars indicate maximum diving depths predicted from Eq. 1.



that the field metabolic rates of Common Murres *Uria aalge*, which spent part of their time resting ashore, averaged 5.2 times the basal metabolic rate (which would be about 5 × SMR) (Laugksch and Duffy 1984).

These data indicate that it is unlikely that the deepest dives could be attained with power outputs less than 2–3 × SMR in alcids and penguins. Furthermore, the calculations assume that the vertical swimming speeds were higher than near-surface cruising speeds and would thus require much greater power outputs, because power requirements are proportional to the cube of velocity in diving birds (Kooyman and Davis 1987). Capture of prey might require additional bursts of speed and hence further reduce aerobic dive times. If metabolic rates did exceed 2–3 × SMR, then the maximum depths recorded could not be attained using purely aerobic metabolism (Fig. 2). Anaerobic metabolism would have to occur, particularly in species such as the two murres and the Razorbill, whose deepest dives were considerably deeper than expected from their body mass (Fig. 1).

The work of Butler and Woakes (1984) and Baudinette and Gill (1985) indicates that nonforaging underwater swimming in penguins is not as demanding as flight in volant seabirds and is considerably more efficient than their surface swimming. Diving birds spend energy to overcome buoyancy, and Butler and Woakes (1984) concluded that the economical diving metabolism in the Little Penguin was partly due to its low buoyancy, relative to ducks. Alcids appear to be less buoyant than most volant seabirds but more buoyant than penguins, and they would have to use additional energy to remain submerged, particularly as they leave the surface. As depths increase, air is forced out of the birds' plumage by increasing pressure, so that their buoyancy and costs of locomotion should decline. There may thus be some energy saved during prolonged dives by going deep. The costs of thermoregulation may rise with increased pressure (Kooyman et al. 1976), but vigorously swimming birds will probably generate excess heat, so this might not be a problem during the dive (Butler and Stephenson 1987).

3.3. Modeling underwater foraging efficiency

Underwater foraging by air-breathing animals can be treated as a central-place foraging problem (Kramer 1988; Ydenberg 1988), and optimal foraging concepts have been applied to diving birds (Wilson and Wilson 1988; Ydenberg and Clark 1989) and whales (Dolphin 1988). I therefore investigated the effect of foraging depth and dive time on foraging efficiency.

In a bird diving with vertical velocity V to feed on prey at a particular depth d, such as schooling fish or benthic prey, the dive cycle consists of dive time (T_d) and recovery time at the surface (T_r), with T_d further divided into vertical travel time (T_t, which is 2d/V) and foraging time (T_f, which is T_d–2d/V). Recovery time is a function of dive time and may be very brief after short aerobic dives but prolonged following longer anaerobic dives, exceeding the dive time severalfold in extreme cases (Jones and Furilla 1987).

Kooyman and Davis (1987) calculated diving efficiency as the proportion of the dive cycle spent underwater (i.e., $[T_f + T_t]/[T_f + T_t + T_r]$) and concluded that this would be maximized if the birds remained within their aerobic depth limits. Ydenberg and Clark (1989), however, pointed out that a better measure of efficiency is the proportion of foraging time (T_f) within each dive cycle

Table 4
Calculations[a] of the foraging efficiency (proportion of dive cycle spent at foraging depth) for Common Murres, assuming vertical velocity of 1 m·s^{-1}

Dive duration (s)	Pause duration (s)	Total cycle (s)	Foraging depth (m)			
			5	10	20	40
(A)						
15	30	45	0.11	0.00	0.00	0.00
40	30	70	0.43	0.29	0.00	0.00
60	30	90	0.56	0.44	0.22	0.00
75	30	105	0.62	0.52	0.33	0.00
85	35	120	0.63	0.54	0.38	0.04
95	40	135	0.63	0.55	0.41	0.11
105	46	150	0.63	0.56	0.43	0.17
115	52	167	0.63	0.57	0.45	0.21
(B)						
15	30	45	0.11	0.00	0.00	0.00
40	30	70	0.43	0.29	0.00	0.00
60	30	90	0.56	0.44	0.22	0.00
70	30	100	0.60	0.50	0.30	0.00
80	30	110	0.64	0.55	0.36	0.00
90	36	126	0.63	0.56	0.40	0.08
100	43	143	0.63	0.56	0.42	0.14
110	52	162	0.62	0.56	0.43	0.19
120	63	183	0.60	0.55	0.44	0.22
130	78	208	0.58	0.53	0.43	0.24
140	97	237	0.55	0.51	0.42	0.25
150	122	272	0.51	0.48	0.40	0.26
160	155	315	0.48	0.44	0.38	0.25
170	199	369	0.43	0.41	0.35	0.24
180	259	439	0.39	0.36	0.32	0.23
190	342	532	0.34	0.32	0.28	0.21
200	458	658	0.29	0.27	0.24	0.18

[a] Two sets of calculations are shown: (A) values used to derive Figure 3, employing the dive:pause ratios from Wanless et al. (1988); and (B) values used to derive Figures 4 and 5, assuming that pause times increase as a power function when dive times exceed 80 s.

(i.e., $T_f/[T_f + T_t + T_r]$). With this criterion, there may be situations in which foraging efficiency might be maximized with deep, anaerobic dives, despite the long delay in recovery at the surface (Ydenberg and Clark 1989).

Foraging efficiency ($T_f/[T_f + T_t + T_r]$) was modeled for the Common Murre, assuming a vertical velocity of 1 m·s^{-1} (D.A. Croll, pers. commun.) and using the dive:pause data given by Wanless et al. (1988). The recovery (pause) times remained relatively constant at 30 s for dives up to 71–80 s but then increased linearly in longer dives (Table 4). For a dive of 60 s to a depth of 20 m, the murre would therefore spend 40 s traveling, 20 s at the foraging depth, and 30 s recovering at the surface, yielding a total dive cycle of 90 s and a foraging efficiency of 0.22 (20/90). Foraging efficiencies calculated from these data for various depths may reach an asymptote as recovery periods start to increase (Table 4, Fig. 3). In shallow waters it may be more efficient for the bird to make more frequent short dives than fewer prolonged dives. This may explain why dive times are often correlated with water depth in shallow inshore areas (Dewar 1924).

It seems unlikely that many of the dive:pause ratios recorded by Wanless et al. (1988) involved anaerobic diving, where pause times tend to increase with a power function instead of linearly (Wilson and Wilson 1988; Ydenberg 1988). A second model of the murre data was therefore run, which assumed that anaerobic metabolism was increasingly involved in dives beyond 80 s (the point at which pause times increase in the data of Wanless et al. 1988). The anaerobic power function is not known for murres, but pause times increased by an exponent of 1.17 in the Pied Cormorant *Phalacrocorax varius* (Wilson and Wilson 1988). Pause times were therefore conservatively assumed to increase exponentially, by $T_r^{1.05}$ for each 10-s increase in dive time beyond 80 s, and foraging efficiencies were calculated for each dive time (Table 4).

Figure 3
Foraging efficiencies in the Common Murre with varying dive times and depths. Efficiencies were computed as the proportion of the dive cycle spent at the foraging depths, assuming a vertical velocity of 1.0 m·s^{-1} and using the dive:pause ratios given by Wanless et al. (1988). See Table 4 for the inputs to the model.

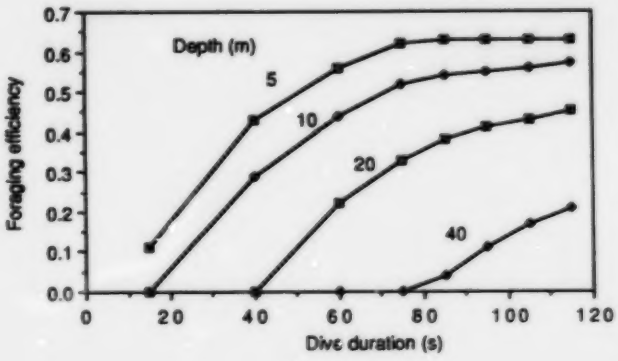
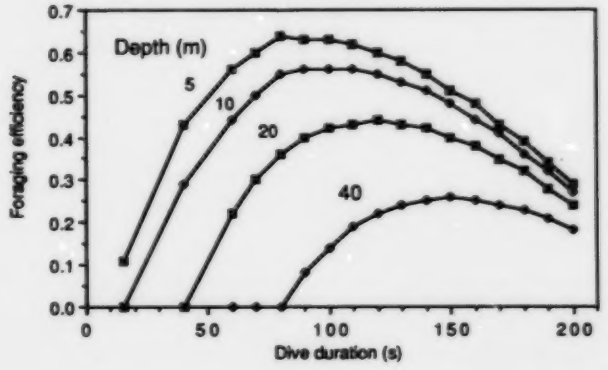


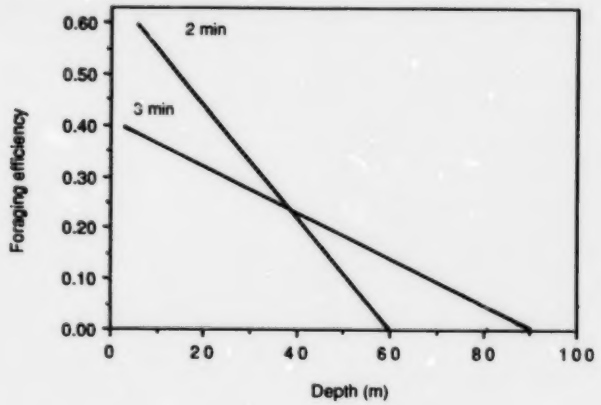
Figure 4
Predicted foraging efficiencies in the Common Murre, calculated as in Figure 3, but assuming that recovery times increase according to a power function, due to increasing anaerobic metabolism, for dives longer than 80 s. See text and Table 4 for details.



With recovery time following a power function, foraging efficiency declines below the asymptote for each depth (Fig. 4). It is now apparent that long, anaerobic dives might be more efficient than shorter dives if the prey are in deep water. This is best shown by plotting foraging efficiency as a function of diving depth, as shown for dives of 2 and 3 min in Figure 5. The two regression lines cross each other at a depth of about 40 m. This shows that for depths of less than 40 m, the 2-min dive is more efficient than the 3-min dive. At depths beyond 40 m, the reverse is true, even though the recovery period after the 3-min dive will be more than 4 times longer than the recovery period after the 2-min dive (Table 4).

These results have important implications for interpreting foraging behaviour. Physiologists concur that most birds appear to avoid anaerobic dives if possible (Kooyman and Davis 1987; Butler and Stephenson 1987), and the glycolytic enzymes in wing muscles of penguins and alcids appear to be suited for sustained aerobic rather than anaerobic glycolysis (Baldwin et al. 1984; Davis and Guderley 1987). Nevertheless, anaerobic diving might at times be a profitable option for a seabird. When foraging on prey at considerable depth, prolonged anaerobic dives may increase overall foraging efficiency by reducing the

Figure 5
Changes in the predicted foraging efficiencies of the Common Murre for dives of 2- and 3-min duration, made to various depths. The slopes were derived from the data in Table 4(B), which assumes that recovery times for such dives would follow a power function. Foraging efficiency would be higher for 2-min dives in depths shallower than 40 m and for 3-min dives at deeper depths.



proportion of time spent traveling underwater. Ydenberg and Clark (1989) showed that anaerobic diving might be profitable if there is a high risk of losing contact with a prey school during trips to the surface. The most efficient foraging, however, will tend to occur when the prey are near the surface and anaerobic dives can be avoided. More data are needed on the swimming speeds and diving energetics of unrestrained seabirds in order to refine this model and to predict accurately in which situations anaerobic diving and lactic acid buildup might be profitable.

3.4. Time-at-depth measurements in penguins and alcids

Several gauges have been developed to measure time-at-depth in seabirds (e.g., Kooyman et al. 1982; Wilson and Bain 1984; Wilson et al. 1989; D.A. Croll, pers. commun.), and the available data have been reviewed to compare maximum diving depths with usual foraging depths in penguins and alcids (Figs. 6 and 7). A significant portion of the diets of Gentoo Penguins *Pygoscelis papua* (Croxall et al. 1988; Wilson 1989) was benthic prey, but the prey of all the other birds sampled here consisted mainly of pelagic fish, crustaceans, and squid. In all cases, virtually all of the foraging was done at depths considerably shallower than the maximum possible and probably within the aerobic dive limits (cf. Fig. 2).

It is not known why these birds occasionally dived much deeper than their usual foraging depths. The most likely explanation is that these were exploratory dives, perhaps facilitating the search for prey by approaching them from below, from where they might be more readily visible (Wilson and Wilson 1990). Exceptionally deep dives might also be undertaken to select large prey items. Among alcids, prey delivered to chicks at colonies are frequently much larger than those eaten by adults at sea (Bradstreet and Brown 1985; Vermeer et al. 1987). In these species, adult birds might seek out the most profitable (large) fish to carry the long distance back to the colony, and occasional very deep, perhaps anaerobic dives might be necessary or most efficient. It is noteworthy that the species that carry single prey items to their chicks (i.e., the two murre species) are those whose maximum depths greatly exceed the general

Figure 6
Diving depth profiles in penguins. Stippled histograms show the proportion of dives that attained each depth interval (from Kooyman et al. 1982; Lishman and Croxall 1983; Croxall et al. 1988). Shaded histograms show the percentage of cumulative dive time spent in each depth interval (from Wilson 1985, 1989). The arrows indicate the maximum depths recorded for each species.

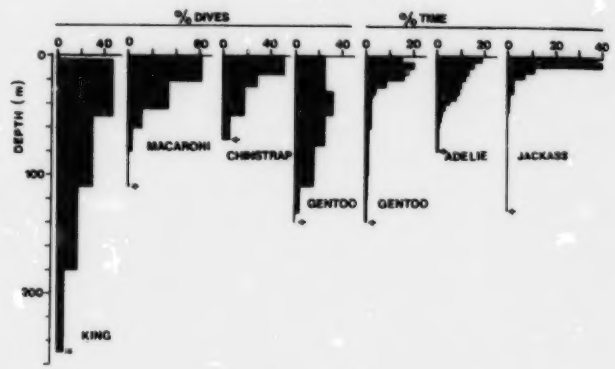
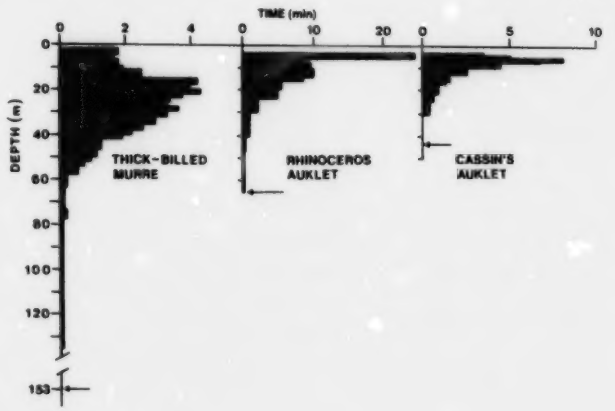


Figure 7
Time-at-depth profiles for alcids. The histograms show the mean cumulative amounts of time spent in each depth interval by 16 Thick-billed Murres (AEB, unpubl. data), two Rhinoceros Auklets (AEB, unpubl. data), and one Cassin's Auklet (Burger and Powell 1990). The arrows indicate the maximum depths recorded for each species.



pattern (Fig. 1). Wilson and Wilson (1988) found that cormorants that took relatively large prey spent more time at deep depths than those taking small prey.

4. Conclusions

This paper confirms the findings of Piatt and Nettleship (1985) and Prince and Harris (1988) that diving abilities of penguins and alcids are strongly influenced by body mass. Significant allometric relationships are reported here for the first time. Other factors, such as prey distribution and sea depth in the foraging range, will also affect diving and should be reported along with diving depths in future studies.

The maximum depths reached by alcids are comparable with those of penguins, although outwardly alcids do not display the same degree of specialization for diving seen in penguins. It is not clear whether the underwater endurance, speed, foraging efficiencies, or abilities to overcome buoyancy of the two groups are similar, but, with the increased interest in diving, this

should soon be known. Research on the physiology and ecology of diving has begun to address the complex interactions that shape a bird's underwater foraging niche.

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Stable isotopic determinations of the trophic relationships of seabirds: preliminary investigations of alcids from coastal British Columbia

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Abstract

The potential for using stable isotopic analysis to determine the trophic position of seabirds was investigated by measuring $\delta^{13}C$ and $\delta^{15}N$ values in lipid-extracted muscle tissue of six Cassin's Auklets *Ptychoramphus aleuticus*, five Tufted Puffins *Fratercula cirrhata*, 12 Ancient Murrelets *Synthliboramphus antiquus*, 19 Marbled Murrelets *Brachyramphus marmoratus*, nine Rhinoceros Auklets *Cerorhinca monocerata*, six Common Murres *Uria aalge*, and five Pigeon Guillemots *Cepphus columba* from coastal British Columbia. Consistent with its largely nektonic diet, Cassin's Auklet showed the least isotopic enrichment, having mean ± SE $\delta^{13}C$ and $\delta^{15}N$ values of -18.5 ± 0.5 and 14.5 ± 0.2‰, respectively. Greatest isotopic enrichment was found for the Pigeon Guillemot, with a mean $\delta^{13}C$ value of -15.7 ± 0.1‰ and a mean $\delta^{15}N$ value of 16.5 ± 0.2‰. Overall, individual $\delta^{13}C$ and $\delta^{15}N$ values ranged from -19.8 to -15.5‰ and from 13.8 to 16.8‰, respectively. Based on $\delta^{15}N$ values, substantial invertebrate contributions to the diets of individual Tufted Puffins, Common Murres, Marbled Murrelets, and Ancient Murrelets are suggested.

Résumé

L'applicabilité de l'analyse des isotopes stables à la détermination du niveau trophique des oiseaux de mer a été étudiée par la mesure des variations (δ) des isotopes ^{13}C et ^{15}N dans les tissus musculaires des oiseaux après extraction des lipides. L'étude a porté sur six Alques de Cassin *Ptychoramphus aleuticus*, cinq Macareux huppés *Fratercula cirrhata*, 12 Alques à cou blanc *Synthliboramphus antiquus*, 19 Alques marbrées *Brachyramphus marmoratus*, neuf Macareux rhinocéros *Cerorhinca monocerata*, six Marmettes de Troïl *Uria aalge* et cinq Guillemots du Pacifique *Cepphus columba* de la côte de la Colombie-Britannique. L'Alque de Cassin a présenté le plus faible enrichissement en isotopes, comme on pouvait s'y attendre en raison de son alimentation constituée principalement d'organismes nectoniques; les valeurs moyennes (erreurs-types) de δ pour cet oiseau sont de -18,5 ‰ (±0,5 ‰) pour le ^{13}C et de 14,5 ‰ (±0,2 ‰) pour le ^{15}N. Le plus fort enrichissement a été observé chez le Guillemot du Pacifique, soit des valeurs moyennes de δ de -15,7 ‰ (±0,1 ‰) pour le ^{13}C et de 16,5 ‰ (±0,2 ‰) pour le ^{15}N. L'ensemble des valeurs mesurées de δ varie de -19,8 à -15,5 ‰ pour le ^{13}C et de 13,8 à 16,8 ‰ pour le ^{15}N. D'après les valeurs de δ pour le ^{15}N, les invertébrés représenteraient une part importante de l'alimentation de Macareux huppés, de Marmettes de Troïl, d'Alques marbrées et d'Alques à cou blanc.

1. Introduction

Knowledge of dietary diversity and overlap in seabird communities is essential to an understanding of their organization and relationships within marine ecosystems. One way in which dietary segregation and potential overlap within these communities can be investigated, at least initially, is through classification of trophic levels. Several authors have used a system of prey trophic levels to better understand the relationships between seabirds and their prey (Knox 1970; Sanger 1972; Ainley and Sanger 1979; Sanger and Jones 1984). Based on earlier work by Mearns et al. (1981), Sanger (1987a) recently advanced the concept of numerical average trophic positions for seabirds that feed at more than one level. His work provided a more precise view of the spectra of trophic levels in seabird diets and allowed trophic relationships of species to be compared on a firmer basis through quantitative analysis. However, Sanger's study, and the majority of dietary investigations of seabirds conducted to date, suffer from several limitations.

Conventional dietary studies depend on the analysis of stomach contents, regurgitations, or pellets found at colonies, or on field observations of foraging birds. Consequently, dietary information is usually short-term and may often be numerically biased against soft-bodied invertebrates or other material that is not easily detected (reviewed by Duffy and Jackson 1986). For dietary studies that require a detailed knowledge of prey choice, these limitations appear unavoidable. Studies concerned with trophic level interaction, however, require estimates of the *proportion* of prey taken from each trophic level.

Investigations of both terrestrial and marine food webs have shown that stable carbon and nitrogen isotope ratios in tissues of consumer organisms are correlated with trophic level (reviewed by Schoeninger and DeNiro 1984; see also Peterson and Fry 1987). Therefore, isotopic analyses of the tissues of seabirds and their prey may provide a useful analytical tool in studies of marine food webs. A brief overview of the application of stable isotopic analysis to dietary investigations is presented here, together with results of isotopic measurements of seabirds from coastal British Columbia.

2. Stable isotopes and food webs

Carbon and nitrogen exist in nature primarily as ^{12}C and ^{14}N, but they also occur in much smaller quantities as the heavy isotopes ^{13}C and ^{15}N. The abundances of these heavy isotopes are expressed in δ notation as parts per thousand (‰) as follows:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and standards are PeeDee belemnite (PDB) ($\delta^{13}C$) and nitrogen in air ($\delta^{15}N$). These values are measured using stable isotope mass spectrometers with internal precisions typically of the order of 0.1‰.

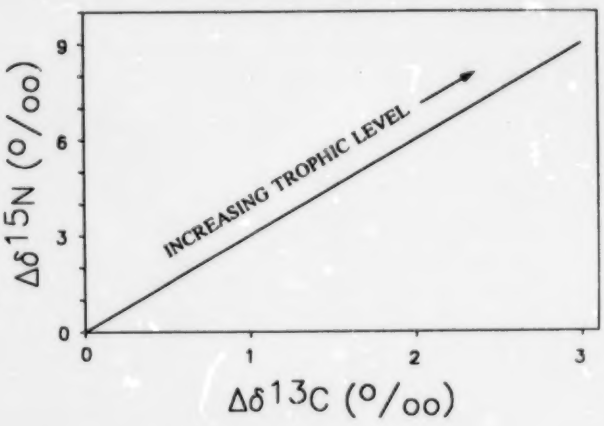
The sources of carbon and nitrogen for marine phytoplankton at the base of the marine food web are usually seawater bicarbonate and dissolved nitrate and ammonia, respectively. Substantial fractionation or change in the isotope ratio of carbon occurs during fixation by photoautotrophs (Craig 1953). Nitrogen fractionation also occurs during primary production, but this process appears to be variable and is less well understood (Cline and Kaplan 1975; Wada 1980).

After primary fixation, further fractionation effects are observed with increasing trophic level (Peterson and Fry 1987). The fractionation values between trophic levels for each element and for various tissue types are not yet established. However, for proteins, in the form of either muscle tissue or bone collagen, $\delta^{13}C$ and $\delta^{15}N$ values appear to be enriched by about 1 and 2–3‰, respectively (reviewed by Schoeninger and DeNiro 1984; Parker et al. 1989). The measurement of both $\delta^{13}C$ and $\delta^{15}N$ values in consumer tissues should, therefore, allow segregation of consumers based on trophic status (Fig. 1). In their isotopic survey of marine organisms, Schoeninger and DeNiro (1984) found that consumers of fish had a mean $^{15}N/^{14}N$ value for bone collagen of 16.5‰, whereas consumers of invertebrates had a mean $^{15}N/^{14}N$ value of 13.3‰.

Isotopic compositions of tissues are a measure of the assimilated (not just ingested) diet. Therefore, tissues with slow and fast turnover rates will reflect long- and short-term diets, respectively. Analysis of bone collagen, for example, should yield historical dietary information that may approach the lifetime average of the individual (Stenhouse and Baxter 1979), whereas analysis of liver tissue or blood should yield dietary information on the order of days to weeks. Because isotope values reflect an actual *integration* of prey types from one or several trophic levels assimilated over time, stable isotope values are trophic indicators, analogous to the numerical average trophic value calculated by Sanger (1987a).

As a preliminary step in determining the usefulness of stable isotopic analysis as an indicator of trophic status in seabirds, I measured isotope values in freezer samples of alcids collected from coastal British Columbia. Within the family Alcidae, individual species are known to differ in their relative dependence on fish and invertebrate prey (e.g., Bédard 1969). I assumed that although fish and invertebrates may overlap trophically depending on size and life history characteristics, alcids feeding on fish generally occupy a higher trophic position than those feeding on invertebrates. Rather than establishing quantitative estimates of relative dietary inputs for each species, my objective was simply to determine if species

Figure 1
Expected pattern of trophic increase of $\delta^{13}C$ and $\delta^{15}N$ values in consumer tissues



could be segregated isotopically and whether this segregation was consistent with current understanding of the diets of different species. Based on the classification of Bédard (1969) and more recent literature, I made some general predictions. Cassin's Auklet *Ptychoramphus aleuticus*, with its largely nektonic diet, was expected to show the least isotopic enrichment. More piscivorous alcids, such as Common Murres *Uria aalge* and Pigeon Guillemots *Cepphus columba*, were expected to show the greatest isotopic enrichment. Intermediate values were expected for Rhinoceros Auklets *Cerorhinca monocerata*, Tufted Puffins *Fratercula cirrhata*, Marbled Murrelets *Brachyramphus marmoratus*, and Ancient Murrelets *Synthliboramphus antiquus*, species that appear to feed on both fish and invertebrate prey.

3. Sample and methods

Muscle tissues of four female and two male Cassin's Auklets, 11 male and eight female Marbled Murrelets, three female and two male Pigeon Guillemots, and four female and five male Rhinoceros Auklets were obtained from birds collected by S.G. Sealy and H.R. Carter in Barkley Sound, B.C., in July–September 1979. Tissues of six Common Murres taken in Masset Inlet, Queen Charlotte Islands, in September–October 1986 were obtained from the collection of the Royal British Columbia Museum. Ancient Murrelet samples were from eight males and four females collected by S.G. Sealy off Oak Bay, Vancouver Island, on 26–31 December 1979. Tufted Puffin samples were from three birds collected on Triangle Island on 27–28 June 1977 (Fig. 2).

Muscle tissue was taken from the left pectoralis, freeze-dried, and powdered to 20 mesh using a Wiley Mill. The lipid was removed from the muscle powder using a Soxhlet apparatus with chloroform solvent for 8 h. This lipid-free powder was then split for nitrogen and carbon stable isotopic analysis. Samples for $\delta^{15}N$ analysis were submitted to the Department of Soil Sciences, University of Saskatchewan, Saskatoon. Samples were converted first to ammonia by Kjeldahl digestion and then to N_2 gas using LiBrOH (Porter and O'Dean 1977). Stable carbon isotopic analysis was performed in the Department of Geology, University of Saskatchewan. Carbon samples were loaded into Vycor tubes with powdered CuO and silver wire and

Figure 2
Sites where alcids used in this study were collected

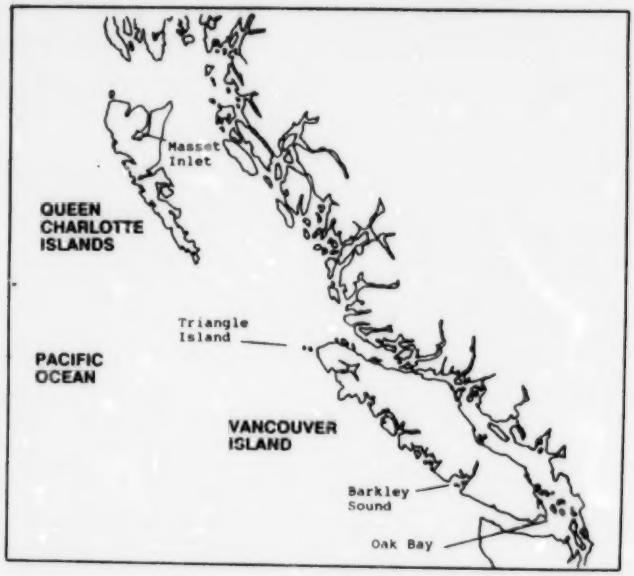
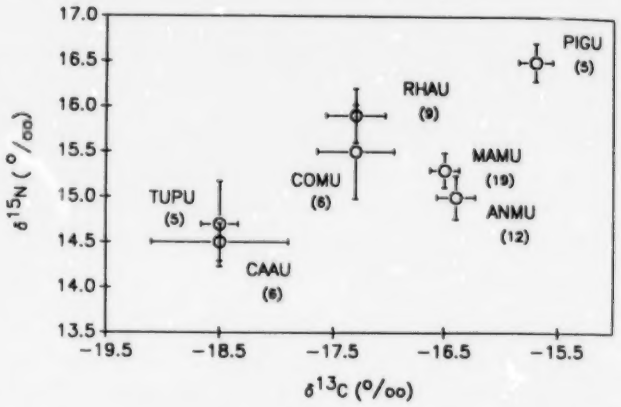


Figure 3
Results of stable isotopic analyses (mean ± SE) of pectoral muscle tissue from alcids collected in coastal British Columbia. CAAU = Cassin's Auklet, TUPU = Tufted Puffin, ANMU = Ancient Murrelet, MAMU = Marbled Murrelet, RHAU = Rhinoceros Auklet, COMU = Common Murre, PIGU = Pigeon Guillemot.



combusted at 850°C for 6 h. The resultant CO_2 was separated and analyzed, as were the nitrogen samples, using a VG Micromass 602 mass spectrometer. Using nitrogen (glycine) and carbon (collagen) laboratory standards, total measurement errors (SD) were estimated as 0.3 and 0.1‰, respectively.

4. Results

Species segregation was established by plotting mean $\delta^{13}C$ and $\delta^{15}N$ values for each species simultaneously (MANOVA: Wilk's Lambda $F = 9.34$, $P < 0.001$) (Fig. 3, Table 1). A Cassin's Auklet showed the lowest $\delta^{13}C$ and $\delta^{15}N$ values of −19.8 and 13.8‰, respectively. The greatest isotopic enrichment occurred in a Pigeon Guillemot sample, with corresponding values of −15.5 and 16.8‰, respectively. Maximum differences in mean isotopic values among species were 2.1‰ for carbon and 2‰ for nitrogen. Maximum isotopic differences among all individuals were 4.3‰ for carbon and 3‰ for nitrogen.

5. Discussion

This study indicates that seabirds may be partially segregated isotopically by $\delta^{13}C$ and $\delta^{15}N$ values in muscle tissues (Fig. 3). Analysis of both isotopes yielded more information than could be obtained from either isotope singly (see also Peterson et al. 1985; Dickson 1986). For example, although nitrogen values for Ancient Murrelets and Tufted Puffins overlapped significantly ($t = 0.52$, $P > 0.5$), their different carbon values ($t = 9.4$, $P < 0.001$) provided species segregation.

Using trophic level enrichment factors of 3‰ for nitrogen and 1.5‰ for carbon, this study indicates mean trophic differences between Cassin's Auklets and Pigeon Guillemots to be 0.7 and 1.9 trophic shifts, respectively. The prediction based on nitrogen results is more convincing. The stable nitrogen isotope values for presumed zooplankton and fish eaters agree closely with those found by Schoeninger and DeNiro (1984). Carbon trophic level enrichment values have been shown to vary from 0 to 2.2‰ (Sackett et al. 1965; Degens et al. 1968; Thayer et al. 1983; Gearing et al. 1984), and Rau et al. (1983) found different values between pelagic and coastal sites. Fry (1988) reported that stable nitrogen enrichments were better trophic indicators than were $\delta^{13}C$ enrichments in investigations of the marine food web on Georges Bank, but interpretation of his results is complicated by the fact that he did not remove lipids from his samples. Recent studies of the trophic relationships of Great Auks *Pinguinis impennis* have also indicated that $\delta^{15}N$ may be more useful than $\delta^{13}C$ in differentiating trophic levels off the coast of Newfoundland (KAH and W.A. Montevecchi, unpubl. data). Further studies are required to determine if this is also true for marine food webs off the coast of British Columbia.

Within species, stable isotope values often varied considerably. Studies of wild (Hobson and Schwarcz 1986) and laboratory-raised (DeNiro and Epstein 1978) animals feeding on isotopically homogeneous diets have shown that individual variation in $\delta^{13}C$ values is of the order of 0.3–0.5‰. Corresponding variation in $\delta^{15}N$ values is not well understood but may be more extensive (DeNiro and Epstein 1981). Most of the variation in isotope values within species implies real dietary differences among individuals. Measurements were made on muscle tissue and thus probably give dietary information on the order of a few weeks. However, samples were usually from birds taken over several months, so temporal changes in diet may be reflected in the interspecific differences reported. Analysis of tissues with shorter isotopic turnover rates is more suited to investigating dietary differences between populations when individuals are collected simultaneously or dietary changes within a population over time.

Isotopic placement of Cassin's Auklet as the lowest trophic level consumer is consistent with current information on its diet. During the breeding season, Cassin's Auklets are primarily zooplankton feeders (Payne 1965; Manuwal 1974). Populations off the B.C. coast feed their chicks euphausiids, calanoid copepods, and juvenile fishes (Vermeer 1981; Vermeer et al. 198[illegible]). Although adult diet is poorly known, Vermeer et al. (1985) suggested that adult birds feed on the same prey that they collect for their young (see also Sanger 1983).

Table 1
Collection information and results of stable carbon and nitrogen isotopic analyses of lipid-extracted pectoral muscle tissues of alcids from British Columbia

Species	Location[a]	Period	n	$\delta^{15}N$[b]	$\delta^{13}C$[b]
Cassin's Auklet	BS	9 July–10 Sept. 1979	6	14.5 ± 0.2	-18.5 ± 0.5
Tufted Puffin	TI	27–28 June 1977	5	14.7 ± 0.5	-18.5 ± 0.1
Ancient Murrelet	OB	26–31 Dec. 1979	12	15.0 ± 0.3	-16.4 ± 0.2
Marbled Murrelet	BS	18 June–19 Dec. 1979, 1980	19	15.3 ± 0.2	-16.5 ± 0.1
Rhinoceros Auklet	BS	6 July–5 Sept. 1979	9	15.9 ± 0.2	-17.3 ± 0.2
Common Murre	MI	27 Sept.–5 Oct. 1986	6	15.5 ± 0.5	-17.3 ± 0.3
Pigeon Guillemot	BS	8 July–6 Sept. 1979	5	16.5 ± 0.2	-15.7 ± 0.1

[a] BS = Barkley Sound, TI = Triangle Island, OB = Oak Bay, MI = Masset Inlet (see Fig. 3).
[b] Mean ± SE.

Isotopic data for Tufted Puffins from Triangle Island overlapped extensively (nitrogen: $t = 0.37$, $P > 0.5$; carbon: $t = 0$, $P > 0.5$) with values obtained for Cassin's Auklets from Barkley Sound, suggesting that the puffins' diet consisted primarily of prey from lower trophic levels. Throughout their range, Tufted Puffins are known to feed their young almost exclusively on fish and occasionally on squid (Vermeer 1979; Wehle 1982). Baird (1987) noted that nonbreeding Tufted Puffins in Alaska ate more invertebrate prey than did breeders. The puffins sampled here were collected during the breeding season, but it is not known whether they were breeders or nonbreeders.

Ancient Murrelets appeared to occupy a higher trophic position than Cassin's Auklets (nitrogen: $t = 1.39$, $P > 0.1$; carbon: $t = 3.97$, $P < 0.002$), suggesting that they fed more on fish. Ancient Murrelets possess longer bills, gapes, and stomachs and have a lower gizzard:proventriculus ratio than Cassin's Auklets, attributes consistent with the capture and digestion of larger, less chitinous prey (Vermeer et al. 1985) (see also Bédard 1969; Sealy 1975).

Based on $\delta^{15}N$ data, Ancient and Marbled murrelets occupied similar trophic positions ($t = 0.84$, $P > 0.2$). Bent (1919) and Kozlova (1957) described the diet of Ancient and Marbled murrelets as consisting primarily of marine invertebrates and fish with some crustaceans (see also Kischinskii 1965). In Barkley Sound, breeding Marbled Murrelets ate primarily juvenile herring and sand lance (Carter 1984). However, Sanger (1987b) found that, in winter, Marbled Murrelets in Kachemak Bay, Alaska, were not as generally piscivorous as once believed (e.g., Bédard 1969).

In the North Atlantic, the diet of Common Murres is considered to consist primarily of fish in all seasons (reviewed by Bradstreet and Brown 1985). Although some invertebrates occur in their diet and may be seasonally important (Bradstreet 1983), captive individuals have been found to reject crustaceans even when no other food was given (Golovkin 1963; Bradstreet and Brown 1985). The species' diet in the North Pacific is even less well known, but recent evidence indicates that crustaceans may be more important than previously realized (Schneider and Hunt 1984; Sanger 1987b). The stable isotope values for the six individuals measured in this study support this contention. Common Murres collected in fall appeared to have a lower trophic relationship than Pigeon Guillemots (nitrogen: $t = 1.87$, $0.1 > P > 0.05$; carbon: $t = 5.06$, $P < 0.001$) and were similar to Rhinoceros Auklets (nitrogen: $t = 0.74$, $P > 0.2$; carbon: $t = 0$, $P > 0.5$). Isotopic values for some individuals overlapped with those for Cassin's Auklets, indicating that this short-term diet may have consisted entirely of crustaceans.

Pigeon Guillemots occupied the highest trophic position isotopically, a result consistent with dietary predictions for *Cepphus* (Bédard 1969). Krasnow and Sanger (1986) determined that adult Pigeon Guillemots from Kodiak Island fed primarily on fish during the breeding season. Bradstreet and Brown (1985) noted that although crustaceans are numerically dominant in diets of congeneric Black Guillemots *Cepphus grylle* in high-Arctic areas, benthic fish made up most of the prey biomass.

6. Recommendations for further study

The present study was conducted without a detailed knowledge of the isotopic compositions of prey organisms within this marine food web and of how these values may vary seasonally or geographically. In areas where mixing of nitrogen or carbon from two isotopically different sources is important, isotopic values will reflect a combination of trophic level effects and source mixing, rather than simply trophic level effects (Fry 1988). For this reason, it may be more appropriate to consider only those species taken in Barkley Sound during summer (i.e., Cassin's Auklet, Marbled Murrelet, Rhinoceros Auklet, and Pigeon Guillemot). Consideration of this subsample does not alter the major findings of this study. Nevertheless, isotopic studies of seabird diets need to be combined with detailed sampling that defines seasonal and spatial variation in isotopic values within those areas where birds are known to feed.

A major limitation in the current application of stable isotopic analysis to investigations of seabird diets is the absence of well-known fractionation factors between diet and various consumer tissues. To date, controlled laboratory studies have been performed on insects, rodents, cats, and rabbits (DeNiro and Epstein 1978, 1981; Tieszen et al. 1983; Chisholm 1986; Tieszen and Boutton 1989). Captive seabirds raised on known isotopic diets could have their tissues measured isotopically. Alternatively, the isotopic measurement of wild seabirds with isotopically narrow diets (e.g., Dovekies *Alle alle*) and their prey would also provide estimates of diet-to-tissue fractionation values. In addition to considering muscle, liver, and bone tissues, the establishment of diet–tissue fractionation factors for blood, feathers, and toenails will also facilitate isotopic dietary investigations that do not involve killing seabirds.

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The distribution of seabirds and fish in relation to ocean currents in the southeastern Chukchi Sea

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Abstract

In late August 1988, we studied the distribution of seabirds in the southeastern Chukchi Sea, particularly in waters near a major seabird colony at Cape Thompson. Foraging areas were characterized using hydrographic data obtained from hydroacoustic surveys for fish. Murres (*Uria* spp.) and Black-legged Kittiwakes *Rissa tridactyla* breeding at Cape Thompson fed mostly on Arctic cod, which are known from previous studies to be the most abundant pelagic fish in the region. Our hydroacoustic surveys revealed that pelagic fish were distributed widely, but densities were estimated to be low (e.g., 0.1–10 $g \cdot m^{-3}$) throughout the study area, and few schools were recorded. Large feeding flocks of murres and kittiwakes were observed over fish schools with densities estimated to exceed 15 $g \cdot m^{-3}$. Fish densities were higher in shallow Alaska Coastal Current waters than offshore in Bering Sea waters, and most piscivorous seabirds foraged in coastal waters. Poor kittiwake breeding success and a low frequency of fish in murre and kittiwake stomachs in late August suggested that fish densities were marginal for sustaining breeding seabirds at that time. Planktivorous Least Auklets *Aethia pusilla* and Parakeet Auklets *Cyclorrhynchus psittacula* foraged almost exclusively in Bering Sea waters. Short-tailed Shearwaters *Puffinus tenuirostris* and Tufted Puffins *Fratercula cirrhata* foraged in transitional waters at the front between Coastal and Bering Sea currents.

Résumé

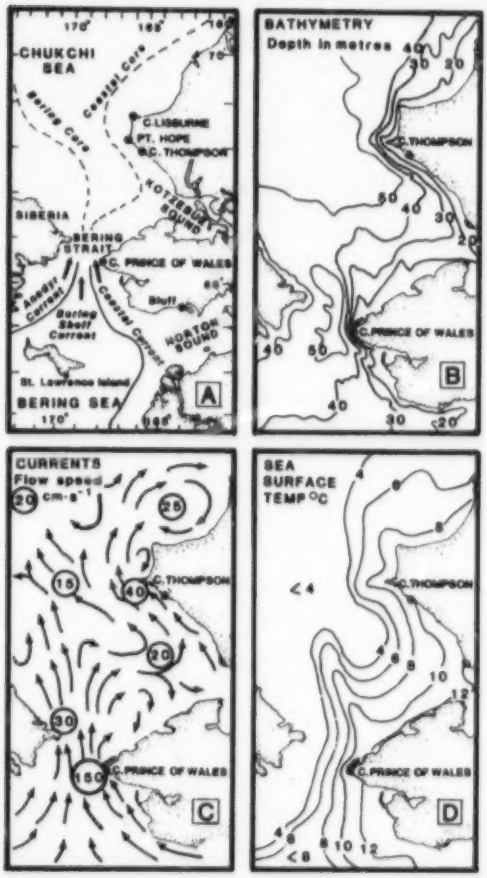
À la fin août 1988, nous avons étudié la distribution des oiseaux de mer dans le sud-est de la mer des Tchouktches, plus particulièrement à proximité d'une importante colonie de ces oiseaux au cap Thompson. Les caractéristiques des zones d'alimentation ont été déterminées à l'aide des données hydrographiques obtenues dans le cadre de sondages hydroacoustiques pour l'étude des poissons. Les marmettes *Uria* spp. et les Mouettes tridactyles *Rissa tridactyla* s'alimentant au cap Thompson se nourrissaient principalement de saïda franc qui, d'après des études antérieures, est le poisson pélagique le plus abondant dans la région. Nos sondages hydroacoustiques ont révélé que les poissons pélagiques sont très répandus, mais que leur densité est faible (0,1–10 $g \cdot m^{-3}$) dans toute la zone d'étude; peu de bancs ont été observés. D'importants groupes de marmettes et de Mouettes tridactyles ont été aperçus au-dessus de bancs de poissons dont la densité estimée dépassait 15 $g \cdot m^{-3}$. La densité des poissons était plus élevée dans les eaux peu profondes du courant côtier de l'Alaska qu'au large dans la mer de Béring, et la plupart des oiseaux de mer piscivores s'alimentaient dans les eaux côtières. Le faible succès de reproduction des Mouettes tridactyles et la fréquence peu élevée des poissons dans l'estomac de celles-ci ainsi que des mouettes à la fin août indiquent que la densité des poissons est alors un facteur marginal pour la survie des oiseaux de mer se reproduisant dans la région. L'Alque minuscule *Aethia pusilla* et l'Alque perroquet *Cyclorrhynchus psittacula*, qui sont des oiseaux planctivores, s'alimentaient presque exclusivement dans la mer de Béring. Les Puffins à bec mince *Puffinus tenuirostris* et les Macareux huppés *Fratercula cirrhata* s'alimentaient dans la zone de transition entre le courant côtier et le courant de la mer de Béring.

1. Introduction

The southeastern Chukchi Sea (Fig. 1) supports a large and diverse seabird fauna during summer. In the Bering Strait, about 1 million planktivorous Least Auklets *Aethia pusilla*, Crested Auklets *A. cristatella*, and Parakeet Auklets *Cyclorrhynchus psittacula*, and five other members of the Alcidae breed on Little Diomede Island and forage in locally productive waters and northwards into the Chukchi Sea (Drury et al. 1981). At Cape Thompson and Cape Lisburne on the northwest Alaska mainland, about 500 000 piscivorous seabirds, mainly Thick-billed Murres *Uria lomvia*, Common Murres *U. aalge*, and Black-legged Kittiwakes *Rissa tridactyla*, breed at colonies and forage locally on schooling pelagic fishes (Springer et al. 1984). Nonbreeding migrants, such as Short-tailed Shearwaters *Puffinus tenuirostris*, move through the Bering Strait into the Chukchi Sea in summer, whereas some terrestrially breeding species, notably phalaropes and jaegers, pass through the Chukchi Sea and forage en route to northern breeding grounds or southern wintering areas. In total, some 25 species of marine birds, including Tufted Puffins *Fratercula cirrhata*, Horned Puffins *F. corniculata*, and Glaucous Gulls *Larus hyperboreus*, regularly reside or forage in the southeastern Chukchi Sea during summer (Swartz 1967; Drury et al. 1981) (Appendix 1).

Productivity in the southeastern Chukchi Sea is elevated during summer and localized by several physical and biological mechanisms (Fleming and Heggarty 1966; Coachman et al. 1975; Springer et al. 1984). The dominant oceanographic feature of the region is the movement of three major currents north through the Bering Strait into

Figure 1
Oceanography of the southeast Bering Sea (adapted from Fleming and Heggarty 1966; Coachman et al. 1975). (A) Place names mentioned in text and major currents. (B) Bathymetric contours. (C) Current directions and flow speeds. (D) Generalized pattern of sea surface temperatures (adjusted with data collected in this study).



the Chukchi Sea (Fig. 1). The Alaska Coastal Current, characterized by warm, low-salinity water, blankets the nearshore zone as it constricts and surges north past Cape Prince of Wales, winds back to the southeast and broadens into Kotzebue Sound, and constricts again along the Alaska coastline from south of Cape Thompson to Cape Lisburne. Bering Shelf and Anadyr waters converge at the Bering Strait to form a core of cold, nutrient-rich, high-salinity Bering Sea water that dominates the south-central Chukchi, pushes eastward against the Alaska Coastal Current north of Kotzebue Sound to Point Hope, and traverses northwest towards the Arctic Ocean. Each current carries northward a unique mixture of nutrients, plankton, and fish that add to, and stimulate, all levels of production in the Chukchi Sea (Springer et al. 1984). Production is also enhanced through local mechanisms. Retreating Arctic ice in June and July provides ice-edge habitat for plankton growth and associated predators, particularly Arctic cod *Boreogadus saida*, the most abundant and widely distributed fish in the southeastern Chukchi Sea (Alverson and Wilimovsky 1966). Sandy substrates maintained nearshore by the Alaska Coastal Current provide habitat for sand lance *Ammodytes hexapterus*, and the warm nearshore waters stimulate growth and production of sand lance and other coastal fishes, including saffron cod *Eleginus gracilis*, herring *Clupea harengus*, and sculpins (Cottidae). Where the Alaska Coastal and Bering Sea currents border, fronts may stimulate local production (Springer et al. 1984).

The main purpose of our study was to determine where breeding birds from colonies at Cape Thompson were foraging in late August 1988 and to identify factors influencing the distribution of seabirds (including nonbreeders and migrants) in the southeastern Chukchi Sea. Data were also collected on seabird and fish distributions around Cape Lisburne and the Diomede Islands. Hydroacoustic surveys for fish were conducted simultaneously with bird surveys to measure the density and distribution of potential prey. Seawater temperature and salinity were measured to characterize water masses and foraging habitats. We collected data on breeding success, diet, and body condition of murres and kittiwakes breeding at Cape Thompson, and we interpret these data in light of information gathered on pelagic fish and bird distributions and from previous studies.

2. Methods

Surveys for seabirds were conducted in the southeastern Chukchi Sea from 23 to 28 August 1988 from the U.S. Fish and Wildlife Service vessel MV 'Tiglax.' Moderate to strong northeasterly winds prevailed throughout the study and limited the collection and interpretation of some data (see below). Except where noted otherwise, seabird censuses were conducted over 10-min intervals from the flying bridge of the MV 'Tiglax' using standard methods for recording species abundance and behaviour (Gould and Forsell 1989). Exact protocols varied depending on the type of survey being conducted (Table 1). When hydroacoustic surveys for fish were conducted simultaneously with bird observations, all birds were counted in a 300-m-wide strip directly in front of the vessel, and the exact time within the census period that birds on the water were observed was noted (except for survey Nos. 1 and 2, in which the strip width was reduced to 150 m, birds were counted over 2-min intervals, and only birds on the water were recorded). Otherwise, all birds were counted in a 300-m-wide strip to the left or right of the ship's centre line, depending on which side offered better viewing conditions (Gould and Forsell 1989). Four of 11 surveys were conducted as arcs around the breeding colonies at Cape Thompson and Cape Lisburne (Table 1, Fig. 2) to determine the directions taken by birds flying to foraging areas. Only flying murres were counted on the first of these arcs (survey No. 4) because of poor lighting conditions, and censuses were conducted over 5-min intervals on other arcs.

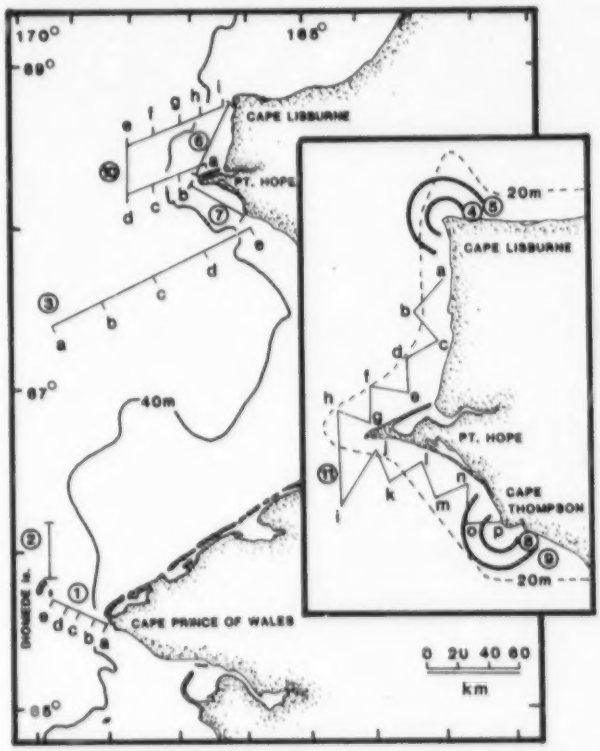
On all surveys, sea surface (3 m depth) temperatures (SST) and salinities (SSS) were monitored using a continuously recording thermosalinograph (Tsurumi Seiki Model 305861, Yokogawa Hokushin Electric Co.). On survey Nos. 1, 3, and 10, water temperature profiles were obtained at the indicated stations (Fig. 2) using a conductivity–temperature–depth (CTD) recorder (Tsurumi Seiki Model 01930 In-situ Water Quality Monitor, Tsurumi Seiki Company Ltd., Yokohama, Japan). The CTD was calibrated in fixed salinity and temperature baths, and the thermosalinograph was calibrated from CTD measurements at 3 m. Additional information on wind speed and direction, sea state, observation conditions, and position

Table 1
Numbers and densities of seabirds observed on surveys in the southeastern Chukchi Sea in August 1988

Survey No.	Date	Survey period[a]	Area (km^2)	All birds		Birds on water		Survey type[b]
				No.	No. km^2	No.	No. km^2	
1	23 Aug.	1425–1845	8.0	—	—	58	7.3	I, H
2	23 Aug.	2140–2340	7.4	—	—	17	2.3	O, H
3	24 Aug.	0725–1555	42.6	452	10.6	27	0.63	O
4	24 Aug.	1625–1135	6.5	570	87.7	—	—	I, A
5	25 Aug.	0815–1020	11.6	2033	175.3	16	1.4	I, A
6	25 Aug.	1045–1315	13.9	675	48.6	55	4.0	I
7	25 Aug.	1915–2130	12.5	581	46.7	20	1.6	I
8	26 Aug.	1310–1425	6.9	695	100.7	11	1.6	I, A
9	26 Aug.	1505–1650	9.7	1394	143.7	24	2.5	I, A
10	27 Aug.	0830–1900	49.9	1450	29.1	77	1.5	O, H
11	28 Aug.	0840–1840	55.5	3874	69.8	650	11.7	I, H
Total or mean			224.5	11802	53.7[c]	955	9.0	

[a] Survey period indicates time from beginning to end of survey, including stops for CTD casts. Ship speed varied with sea state.
[b] I = inshore, O = offshore, A = arc around colony, H = hydroacoustic survey conducted simultaneously.
[c] Arcs around colonies excluded from calculation.

Figure 2
Surveys conducted in the southeastern Chukchi Sea in August 1988. Numbers in circles indicate survey number (see Table 1). Lower-case letters along survey Nos. 1, 3, and 10 indicate location of CTD stations; those along survey No. 11 (inset) indicate location of waypoints.



were noted at the beginning of each census period (Gould and Forsell 1989).

Hydroacoustic surveys were conducted using a BIOSONICS Model 102 Echosounder and a hull-mounted 120-kHz dual-beam transducer (4 m below the surface). Transmit power was set at 217 dB, gain at -125.4 dB, bandwidth at 5 kHz, trigger interval at 0.5 s, and pulse width at 0.5 ms for all surveys. Fish echo signals were integrated in real time over 2-min time intervals and 10-m depth intervals using a BIOSONICS Model 121 Digital Echo Integrator with 20 LogR amplification. Integration thresholds were set at 100 mV for each depth stratum. Signals were integrated in relative voltage units, downloaded onto a microcomputer, and later converted to estimates of fish density and abundance. Integrations of echo signals in the upper 10 m of the water column were not used to calculate fish densities because rough seas introduced air bubbles into the water column and produced excessive surface noise most of the time.

Assuming that Arctic cod were the most abundant fish in the area (Alverson and Wilimovsky 1966) and using the average size of Arctic cod consumed by seabirds at Cape Thompson (see Results), we used a target strength of $-64\ dB \cdot g^{-1}$, calculated from regression equations for fish with closed swimbladders (physoclists), to estimate absolute from relative fish densities (Thorne 1983; Foote 1987). In situ measurements of Arctic cod target strengths in Lancaster Sound indicate that this is a good estimate (R. Crawford, pers. commun., Fisheries and Oceans Canada, Winnipeg), and it is very close to target strengths determined in situ for capelin *Mallotus villosus* and Atlantic cod *Gadus morhua* in eastern Canada (Rose and Leggett 1988; D. Miller, pers. commun., Fisheries and Oceans Canada, St. John's). In the absence of trawl samples to identify and measure fish targets, however, the fish densities presented here must be considered approximate. One other forage fish likely to have been encountered in August was sand lance (Springer et al. 1984). There are no published estimates for sand lance target strengths, but because they have "open" swimbladders (physostomes), it is likely that target strengths are about 5–10 dB lower than those of cod and capelin (Foote 1987; Rose and Leggett 1988). This would lead to an underestimate of fish densities where sand lance were recorded (only nearshore) (Alverson and Wilimovsky 1966; Springer et al. 1984). Another potential source of error was the inclusion of zooplankton signals in echo integrations. However, zooplankton have much lower target strengths than fish (e.g., -80 to -100 dB) and, with the integration (noise) threshold set at 100 mV, would have made a negligible contribution to integration values (Greenlaw 1979). Faint zooplankton scattering layers were recorded on echograms, however, with the chart recorder threshold set at 30–50 mV.

We collected murres and kittiwakes for diet studies by shooting them as they returned to the colony. Birds were weighed, and the amount of subcutaneous and mesenteric fat was estimated visually (scale 0–3) (Gaston et al. 1983). Stomachs and gizzards were removed and stored in 50% ethanol solution for later examination. Stomach contents were sorted and identified in the laboratory using appropriate taxonomic keys and reference material (A. Springer, Institute of Marine Science, University of Alaska, Fairbanks). The sizes of most fish prey recovered were reconstructed from regressions of fish length on otolith length and of fish weight on fish length (for details, see Springer et al. 1984).

The measurement of fish and seabird aggregations, and correlations between them, depends on the spatial scale at which data are collected and analyzed (Schneider and Piatt 1986; Piatt 1990). Therefore, correlations were examined over a range of scales, from the minimum measurement scale (i.e., 2, 5, or 10 min, depending on the survey, where time is equivalent to distance traveled: e.g., 1 min = 0.3 km at a ship speed of 10 kn) to larger scales

(i.e., 10, 20, 40, or 80 min, depending on the total survey length, with at least four data points for measuring correlations). Correlations between fish or birds and gradients in SST or SSS were similarly examined. Gradients were calculated by lagging temperature or salinity measurements by one measurement interval (e.g., 10 min) and taking the absolute value of the difference between successive observations as the gradient. Correlations between birds, fish, and gradients were measured at equivalent scales using Spearman rank correlation.

The affinity of different seabird species for different water types was examined by grouping 10-min bird observations according to whether they occurred in Bering Sea/Anadyr water (SST < 7.5°C, SSS > 31‰), transitional water (SST ≥ 7.5°C, SSS > 30‰), or Alaska Coastal water (SST ≥ 8.0°C, SSS < 30‰) as determined by the continuously recording thermosalinograph. The categorization of Bering Sea/Anadyr and Alaska Coastal water types by sea surface characteristics is based on definitions in Coachman et al. (1975), which differ from definitions based on CTD profiles of the entire water column because surface waters are warmer and less saline than underlying water. Our boundaries on the "transitional" water type are fairly arbitrary, however, and by definition represent the type of water found in mixed frontal zones between the well-defined Alaska Coastal and Bering Sea currents. Flying birds from arc and inshore surveys near Cape Thompson were excluded from this analysis, because those birds could have been flying over Coastal waters to get to foraging areas offshore.

3. Results

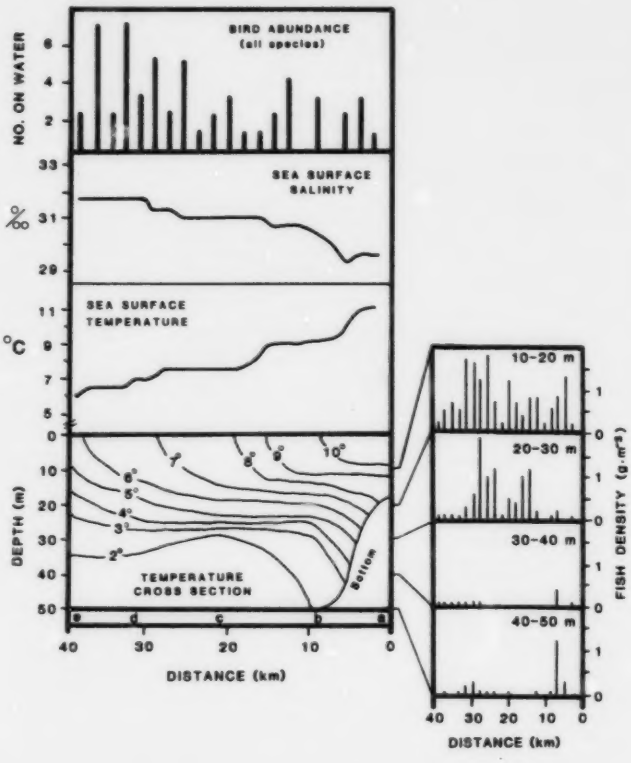
3.1. Bering Strait

On survey No. 1, we crossed the strait from Cape Prince of Wales to Little Diomede Island (Fig. 2). Thermosalinograph and CTD profiles revealed a marked temperature–salinity gradient from east to west and a thermocline at a depth of about 30 m (Fig. 3). Zooplankton were concentrated just above the thermocline, and estimated fish densities of up to about 2 g·m^{-3} were recorded in the 10–30-m layer. The density of birds on the water during this survey was higher than densities observed on all subsequent surveys except for coastal survey No. 11 at Cape Thompson (Table 1). In decreasing order of abundance, Parakeet Auklets, Common Murres, Tufted Puffins, and Glaucous Gulls accounted for 74% of birds observed on the water.

At the minimum measurement scale of 0.36 km and over larger scales (up to 9 km), there were no significant correlations between total birds and fish densities in any depth stratum. The surface layer (5–10 m) was excluded from this and subsequent analyses because surface signals were due to air bubbles introduced by turbulence, not to fish echoes. The "density" of signals in the uppermost stratum was significantly correlated with wind speed ($r = 0.85$, $n = 20$, $P < 0.0001$) and sea state ($r = 0.77$, $n = 20$, $P < 0.0001$).

On the survey north from Little Diomede Island (survey No. 2, Fig. 2), there was little variation in SST (6–8°C) or SSS (30.6–31.3‰) from beginning to end. Average fish densities were between 0.04 and 0.15 g·m^{-3} in the 10–40-m depth strata. Few birds were observed, of which 75% were Least, Parakeet, and Crested auklets. Most auklets were observed within 10 km of Little Diomede Island.

Figure 3
Observations of seabirds, fish, and hydrography on survey No. 1 across the Bering Strait. Lower-case letters at bottom correspond to CTD stations shown in Figure 2. Histogram at lower right shows fish densities at different 10-m depth strata along the survey track.



3.2. Crossing the southeastern Chukchi Sea

We crossed the southeastern Chukchi Sea from about 150 km west-southwest to about 10 km south of Cape Thompson (Fig. 2). Thermosalinograph and CTD profiles revealed that the survey started in the tongue of Alaska Coastal water that extends about 200 km north of Bering Strait (Fig. 1), crossed the broad band (approximately 80 km) of stratified Bering Sea water that intrudes towards Kotzebue Sound, and ended in the Alaska Coastal Current (about 50 km wide). Fronts between Alaska Coastal and Bering Sea waters, defined by large SST and SSS gradients and vertically mixed waters (Coachman et al. 1975), were observed at distances of 10–20 and 100–110 km along the survey track (Fig. 4). Hydroacoustic surveys were not conducted because of rough seas. Only 6% of birds observed were on the water, and the density of flying birds was lower than on any other survey (Table 1).

Nonetheless, some patterns were evident. Most Parakeet Auklets were observed at a front between Alaska Coastal and Bering Sea waters. Most phalaropes (of which 78% were identified as Red Phalaropes *Phalaropus fulicaria*) and Least Auklets were found over stratified Bering Sea waters. Murres were most abundant in Alaska Coastal waters within about 60 km of Cape Thompson. No significant correlations between birds and temperature–salinity gradients were found.

3.3. Radial arcs around Cape Thompson and Cape Lisburne

Radial surveys around Cape Thompson revealed that most murres and kittiwakes were flying to the

Figure 4
Observations of seabirds and hydrography on survey No. 3 across the southeastern Chukchi Sea. Lower-case letters at bottom correspond to CTD stations shown in Figure 2.

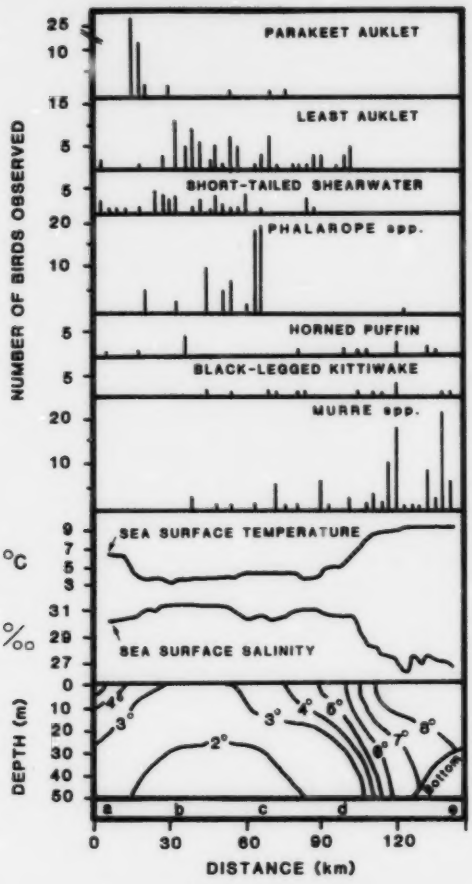
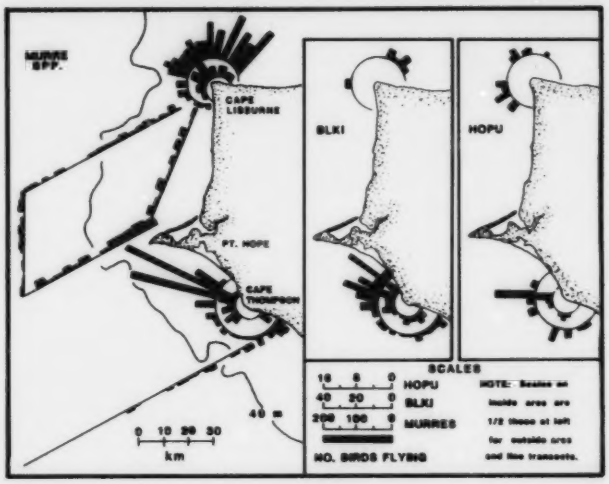


Figure 5
Murre, kittiwake (BLKI), and Horned Puffin (HOPU) flight directions from Cape Thompson and Cape Lisburne as determined from arc surveys around the colonies. Numbers of murres flying on offshore surveys (Nos. 3 and 10) are also shown.



northwest on 26 August and that a small proportion were flying southeast along the coast (Fig. 5). Horned Puffins flew mostly to the west and south of Cape Thompson. Surveys around Cape Lisburne revealed that most murres and kittiwakes flew to the northwest, north, and especially northeast. Again, Horned Puffins flew to different foraging areas than did murres and kittiwakes.

3.4. Offshore from Point Hope to Cape Lisburne

With evidence from the radial arc surveys and two coastal surveys (Nos. 6 and 7) that most birds from Cape Thompson were flying to the west and north of Point Hope, we conducted a survey (No. 10) to encompass potential foraging areas up to about 90 km west and 110 km northwest of Cape Thompson (Fig. 2). Thermosalinograph and CTD profiles revealed that the Alaska Coastal Current was constricted to a narrow band about 30 km wide off Point Hope (Fig. 6, CTD stations a–d) and was broader (about 40 km) off Cape Lisburne (Fig. 6, CTD stations e–i). SST and SSS gradients were stronger at the front between Alaska Coastal and Bering Sea waters off Point Hope than off Cape Lisburne.

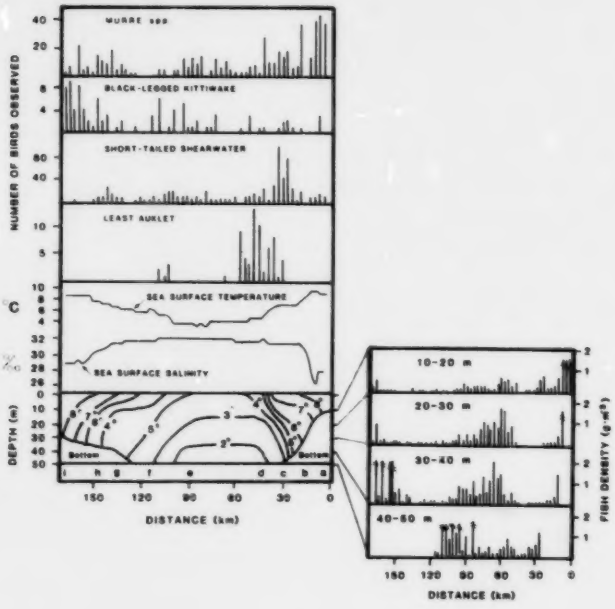
Fish density and distribution varied markedly between water masses (Fig. 6). In shallow, stratified Alaska Coastal waters at Point Hope, estimated fish densities were relatively high (up to 23 $g \cdot m^{-3}$), and most fish were distributed near the bottom or in midwater. Average fish density was estimated to be 1.6 $g \cdot m^{-3}$, and total fish biomass was estimated to be 35.5 $mt \cdot km^{-2}$. Moving offshore into the vertically mixed transitional waters between Alaska Coastal and Bering Sea waters (about 10 km on either side of CTD station c, Figs. 2 and 6), fish were conspicuously absent. Further offshore in stratified Bering Sea water, and moving north between CTD stations d and e, moderate fish densities (1–2 $g \cdot m^{-3}$) were recorded at depths of 20–40 m. In transitional and Bering Sea waters, estimated fish densities averaged 0.073 $g \cdot m^{-3}$, and fish biomass in the 10–40-m strata was estimated to be 2.19 $mt \cdot km^{-2}$. Upon returning inshore to Cape Lisburne (CTD stations e–i), estimated fish densities declined again dramatically in transitional waters (between CTD stations f and g) before rising again to much higher levels (up to 249 $g \cdot m^{-3}$) near the bottom in Alaska Coastal waters. Estimated fish densities in this area averaged 1.26 $g \cdot m^{-3}$, and total biomass was estimated to be 11.5 $mt \cdot km^{-2}$ in the 10–40-m strata.

At a 6-km spatial scale, there was a significant negative correlation between fish density and SST gradients in two of four depth strata examined (20–30 m: $r = -0.45$, $n = 28$, $P = 0.02$; 30–40 m: $r = -0.45$, $n = 28$, $P = 0.02$). Negative correlations between fish density and SSS gradients were generally weaker and insignificant (except for the 20–30-m stratum: $r = -0.40$, $n = 28$, $P = 0.03$). This analysis corroborates the visual impression of Figure 6 that fish were scarce in the front between Alaska Coastal and Bering Sea currents.

At a spatial scale of 6 km, murres on the water (3% of total observed) were strongly correlated with fish density in the 10–20-m stratum ($r = 0.82$, $n = 28$, $P = 0.0008$) and the 10–30-m strata ($r = 0.60$, $n = 28$, $P = 0.03$). Reflecting the negative relationship between fish density and SST gradients, the number of murres on the water was also negatively correlated with SST gradients ($r = -0.79$, $n = 28$, $P = 0.04$) at a 6-km spatial scale.

Kittiwakes were not correlated with fish density in any depth stratum at any spatial scale. Only one kittiwake was observed on the water, and no feeding flocks were

Figure 6
Observations of seabirds, fish, and hydrography on survey No. 10 northwest of Cape Thompson. Lower-case letters at bottom correspond to CTD stations shown in Figure 2. Histogram at lower right shows fish densities in different 10-m depth strata along the survey track (broken bars indicate density values exceeding 2 g·m^{-3}, with values of 3–4 g·m^{-3} in the 10–20-m stratum; 23 g·m^{-3} in the 20–30-m stratum; 12–249 g·m^{-3} in the 30–40-m stratum; 4–80 g·m^{-3} in the 40–50-m stratum).



observed, however, so it was impossible to identify birds that were potentially foraging for this analysis. Like murres, however, kittiwakes were negatively correlated with SST gradients at both small (3 km: r = –0.38, n = 56, P = 0.03) and large (18 km: r = –0.90, n = 9, P = 0.04) spatial scales. Most kittiwakes were observed on approach to Cape Lisburne (Fig. 6), and the arc surveys (Fig. 5) suggest that those kittiwakes came from Cape Thompson rather than Cape Lisburne.

The only other seabirds seen in abundance were Short-tailed Shearwaters and Least Auklets. In contrast to murres, shearwaters and auklets were negatively correlated with fish abundance in most depth strata at a 6-km scale, although correlations were significant with fish only in the 30–50-m strata (auklet: r = –0.49, n = 24, P = 0.05; shearwater: r = –0.58, n = 24, P = 0.009). Most (81%) of the Least Auklets observed were swimming and were found on the Bering Sea side of the front between the Alaska Coastal and Bering Sea currents (Fig. 6). In contrast to murres and kittiwakes, Least Auklet numbers were positively correlated with SST gradients (r = 0.78, n = 28, P = 0.02) and SSS gradients (r = 0.83, n = 28, P = 0.04) at a 6-km spatial scale. All the shearwaters observed were flying; although they were dispersed over a wide area, the largest aggregations were found on the Alaska Coastal Current side of the front (Fig. 6). Shearwater numbers were not well correlated with property gradients.

3.5. Coastal survey

On 27 August and about 80 km south of Cape Lisburne, we encountered the first of only three large murre and kittiwake feeding aggregations observed during the study. About 4 km from shore, we passed over a small, dense school of fish on which about 500–700 murres, 25 kittiwakes, and 10 Glaucous Gulls were actively feeding. The echogram trace of this school was qualitatively different from all previous fish traces and similar to traces of known sand lance schools recorded in the Aleutians in the summer of 1988 (JFP, unpubl. data). On 28 August, we surveyed the shallow nearshore zone in a zigzag pattern from about 30 km south of Cape Lisburne to Cape Thompson (Fig. 2).

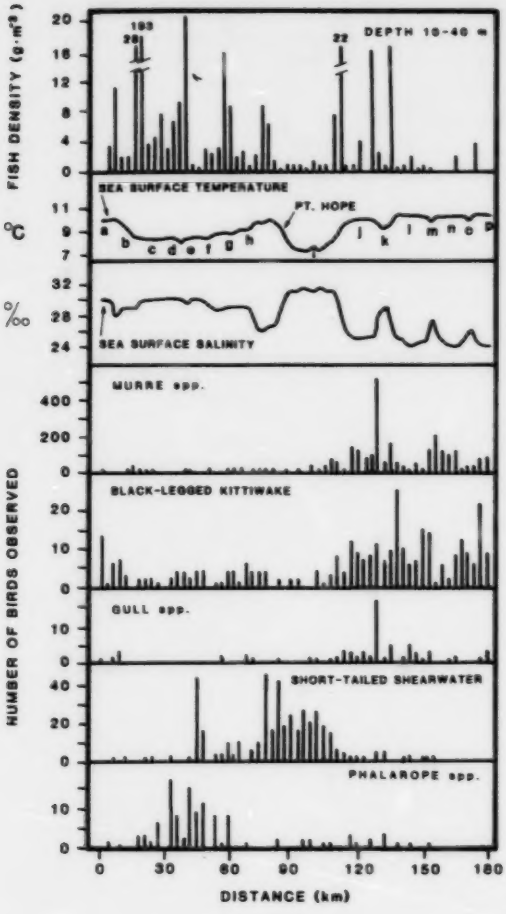
Thermosalinograph records indicated that north of Point Hope (waypoints a–h, Fig. 7), waters within the 20-m bathymetric contour (Fig. 2) were a nonhomogeneous mix of Alaska Coastal water and transitional or Bering Sea water. Alaska Coastal water predominated as we rounded Point Hope (after waypoint h), where temperatures increased and salinities decreased rapidly. Immediately south of Point Hope, cold, high-salinity transitional water predominated beyond the 20-m contour (waypoint i) and bordered (waypoints k, m, and o) with Alaska Coastal waters along the 20-m contour all the way to Cape Thompson. These observations are consistent with previous oceanographic studies of the area (Coachman et al. 1975): the Alaska Coastal Current is compressed by the Bering Sea Current as both traverse north past Point Hope, with greater mixing of the two water masses in a gyre north of Point Hope.

In the 10–20-m stratum, fish density was not correlated with SST or SSS gradients at any spatial scale. In the 20–30-m stratum, where the densest fish aggregations were found both north and south of Point Hope, fish density was positively correlated with SST gradients at a spatial scale of 3 km (r = 0.36, n = 62, P = 0.01). In the 30–40-m stratum, fish density was positively correlated with SST and SSS gradients at all spatial scales but reached a maximum at a scale of 12 km (SST: r = 0.69, n = 15, P = 0.01; SSS: r = 0.78, n = 15, P = 0.0009). Fish schools were densest on the coastal side of the border between Alaska Coastal and transitional waters, where temperatures and salinities changed rapidly, and were largely absent in the cold core of transitional water off Point Hope (waypoint i).

Over the whole survey area, estimated fish densities averaged 0.59 g·m^{-3}, and total biomass was estimated to be 5.3 mt·km^{-2} in the 10–30-m strata. However, fish densities north of Point Hope were generally higher over a larger area (estimated average density of 1.3 g·m^{-3}) than south of Point Hope (0.18 g·m^{-3}). North of Point Hope, at least five aggregations with densities greater than 10 g·m^{-3} and one school with a density of 193 g·m^{-3} were encountered (Fig. 7). No significant seabird feeding aggregations (i.e., more than five birds in a flock on the water) were found north of Point Hope. South of Point Hope, however, one large aggregation of murres (466), kittiwakes (10), and Glaucous Gulls (15) was found feeding actively on a school of fish that ranged from the surface to the bottom and had a maximum density of 14.3 g·m^{-3} in the 20–30-m stratum. From the echogram trace, this appeared to be a school of sand lance. If so, calculated densities would be higher (i.e., 70–140 g·m^{-3}), because sand lance have a lower target strength than most other fish likely to be encountered inshore (see Methods). One other seabird aggregation (41 murres, three kittiwakes, three gulls) was observed on the water above a similar school with densities of 16.5 g·m^{-3}.

It appeared that, with the exceptions noted above, many dense fish aggregations were not exploited by foraging seabirds (Fig. 7). Nonetheless, murres on the water (20% of 2922 birds) were significantly correlated with fish

Figure 7
Observations of seabirds, fish, and hydrography on coastal survey No. 11 north of Cape Thompson. Lower-case letters along sea surface temperature profile correspond to waypoints shown in Figure 2. Histogram at top shows fish densities summed over 10–40-m depth strata.



density in the 20–30-m stratum at intermediate spatial scales (12 km: r = 0.54, n = 15, P = 0.02). Similarly, kittiwakes on the water (6% of 326) were positively correlated with fish in the 20–30-m stratum at the same scale (r = 0.71, n = 15, P = 0.002). Murres were not correlated with temperature–salinity gradients at any spatial scale, and kittiwakes were weakly correlated with SST gradients at a 3-km scale (r = 0.27, n = 62, P = 0.04).

Most identified gulls were Glaucous Gulls, and their numbers were not correlated with fish densities. Like kittiwakes, however, gulls on the water (32% of 72 birds) were weakly correlated with SST (r = 0.27, n = 62, P = 0.04) and SSS (r = 0.34, n = 62, P = 0.01) gradients at the minimum spatial scale of 3 km. As expected from their distributions, neither shearwaters nor phalaropes were correlated with fish densities. Shearwaters were positively correlated with temperature gradients at intermediate spatial scales (6 km: r = 0.40, n = 31, P = 0.03; 12 km: r = 0.53, n = 15, P = 0.04). In marked contrast to murres and kittiwakes, shearwaters were concentrated in transitional waters off Point Hope (Fig. 7). In contrast to all other species, phalaropes (only Red Phalarope identified) were concentrated in an area just north of Point Hope (Fig. 7).

3.6. Summary: seabird affinities with water types

Numbers of the most abundant species observed during 10-min intervals on all surveys were superimposed on sea surface temperature–salinity diagrams to assess not only what water types were frequented by those species, but also where the largest aggregations occurred (Fig. 8). For example, whereas Short-tailed Shearwaters were widely distributed over all water types, many of the largest aggregations were found in transitional waters. Similarly, the largest kittiwake and Common Murre aggregations were located in Coastal waters. Thick-billed Murres were found in all water types. Least Auklets were restricted almost entirely to Bering Sea and transitional waters, and the largest aggregations were observed in high-salinity, low-temperature Bering/Anadyr water.

Using data adjusted for survey effort in each water type, we assessed the affinity of common species for each water type (Fig. 9) by testing (Chi-square) the hypothesis that birds were equally distributed among water types. This hypothesis was rejected for all species except Tufted Puffin (STSH $\chi^2 = 156.1$, $P < 0.0001$; COMU $\chi^2 = 69.4$, $P < 0.0001$; TBMU $\chi^2 = 38.7$, $P < 0.0001$; TUPU $\chi^2 = 1.17$, ns; HOPU $\chi^2 = 12.0$, $P = 0.002$; LEAU $\chi^2 = 67.7$, $P < 0.0001$; PAAU $\chi^2 = 12.5$, $P = 0.002$; BLKI $\chi^2 = 39.4$, $P < 0.0001$; GULL $\chi^2 = 63.8$, $P < 0.0001$; PHAL $\chi^2 = 101.8$, $P < 0.0001$; df = 2 in all cases). Birds with an affinity for Coastal waters included both murres, Horned Puffins, kittiwakes, gulls, and phalaropes (Fig. 9). Short-tailed Shearwaters exhibited a strong affinity for transitional waters, and most Tufted Puffins were also found in transitional waters. Least and Parakeet auklets were found mostly in Bering Sea/Anadyr water, and Parakeet Auklets showed a slight preference over Least Auklets for Coastal water ($\chi^2 = 9.1$, df = 2, $P < 0.05$). Similarly, a significantly higher proportion of Thick-billed Murres compared with Common Murres foraged in transitional and Bering Sea/Anadyr waters ($\chi^2 = 17.7$, df = 2, $P < 0.001$).

3.7. Diets and condition of seabirds at Cape Thompson

Murres and kittiwakes collected at Cape Thompson in July and August fed predominantly on schooling fishes, of which Arctic cod was most important by frequency of occurrence or percentage wet weight (Table 2). The average (± SD) length of Arctic cod taken by all species was 157 ± 38 mm (n = 202), with an extrapolated average weight of about 31 g. Thick-billed and Common murres also fed frequently on sand lance, saffron cod, and sculpins, but these contributed little to the total mass of food consumed because of their low numbers or relatively small average masses (about 6.7, 23, and 4.8 g, respectively). Thick-billed Murres also fed on invertebrates, and they are probably underrepresented in diets owing to their rapid digestion (Springer et al. 1984). Only kittiwakes consumed herring, which were abundant nearshore in July and early August. Herring consumed by kittiwakes were estimated to be about 200 mm in total length and 100 g in weight (Whitmore and Bergstrom 1983). Kittiwakes had obvious difficulty swallowing such large fish. Herring were apparently too large for murres to handle or swallow, and murres ignored herring schools around Cape Thompson.

The numbers of fish (or otoliths) found in bird stomachs varied markedly throughout the breeding season (Table 3). Arctic cod predominated in diets in early to mid-July, then declined markedly by mid- to late August. Sand lance, saffron cod, and herring were also consumed in smaller quantities. Birds had proportionately more food in

Figure 8
Sea surface temperature–salinity diagram of all waters sampled on surveys in the southeastern Chukchi Sea, and the distribution and abundance of selected seabird species within different water types (see Methods for definition of water types). Species codes: LEAU = Least Auklet, COMU = Common Murre, TBMU = Thick-billed Murre, BLKI = Black-legged Kittiwake, STSH = Short-tailed Shearwater.

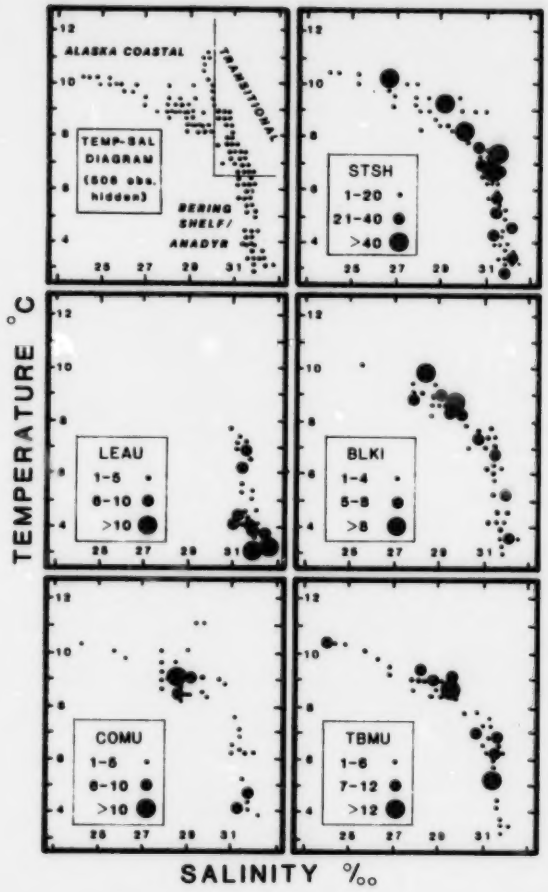
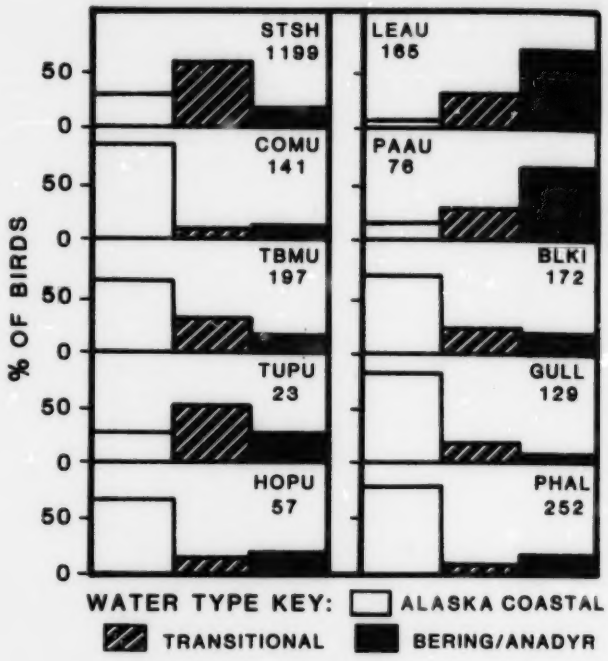


Figure 9
The proportion of seabirds observed in different water types in the southeastern Chukchi Sea (proportions weighted by the total area surveyed in each water type). Species codes: TUPU = Tufted Puffin, HOPU = Horned Puffin, PAAU = Parakeet Auklet, GULL = gull spp., PHAL = phalarope spp.; for other codes, see Figure 8 caption.



their stomachs in July than in August (Table 3), and most empty stomachs were found in August (Table 2).

Murre and kittiwake body masses declined between July and August, although the difference was significant only for male Thick-billed Murres and kittiwakes (Table 4). The body masses of Common Murres, Thick-billed Murres, and kittiwakes (male only) declined by 4, 8, and 11%, respectively. Fat deposits in both murre species increased or remained stable between July and August, whereas kittiwake fat deposits decreased significantly.

4. Discussion

Two oceanographic features of the southeastern Chukchi Sea figured prominently in our study of the distribution and abundance of seabirds and their prey. First, the presence of two distinct water masses (Bering Sea/Anadyr and Alaska Coastal currents) and the front between them resulted in three distinct marine habitats. Second, sea ice disappeared from the area later in 1988 than in any previous year of study (BSF, unpubl. data), and SSTs were about 1–2°C colder than those reported by Fleming and Heggarty (1966) and Coachman et al. (1975).

Below, we consider the influence of these oceanographic conditions in our discussions of:
(1) potential forage fish distribution and abundance;
(2) foraging ecology and distribution of breeding and migrating seabirds; and
(3) the relationship between foraging and breeding success of seabirds at Cape Thompson.

4.1. Forage fish distribution and abundance

It is likely that most of the prey recorded on hydroacoustic surveys were Arctic cod. Extensive trawl surveys conducted throughout the study area in August 1959 revealed that Arctic cod were by far the most abundant and widely distributed fish in the region: numbers caught exceeded those of other common fishes by at least 1–2 orders of magnitude (Alverson and Wilimovsky 1966). There is no indication from predator studies that the forage fish fauna has changed substantially since these trawl surveys were conducted (Divoky 1978; Lowry and Frost 1981; Springer et al. 1984; Bradstreet et al. 1986; this study), and there are no fisheries for Arctic cod. A variety of flatfishes (Pleuronectidae) and sculpins are common in the area, but most of these demersal fishes would not have been detected by our hydroacoustic surveys. However, other common pelagic species, such as capelin (offshore) and saffron cod (inshore), may have contributed to our estimates of fish density. As those species are also consumed by seabirds, are similar in size to Arctic cod, and have similar target strengths (Foote 1987; Rose and Leggett 1988), our estimated forage fish densities were probably not biased much by using Arctic cod target strengths. Indeed, "fish with swimbladders appear to constitute a single class with respect to target properties" (Thorne 1983).

Table 2
Occurrence of major taxa in diets of Thick-billed Murres (TBMU), Common Murres (COMU), and Black-legged Kittiwakes (BLKI) at Cape Thompson in summer 1988[a]

Parameter	TBMU		COMU		BLKI	
	n	%	n	%	n	%
Number examined	46	(100)	14	(100)	18	(100)
Number empty	15	(33)	1	(7)	2	(11)
Frequency of invertebrates	5	16	0	0	3	19
Frequency of fish	30	97	13	100	14	88
Number of individuals						
Arctic cod	125	78	58	89	22	71
Saffron cod	5	3	2	3	0	0
Sculpins	4	2	1	2	0	0
Herring	0	0	0	0	5	16
Sand lance	18	11	1	2	0	0
Unidentified fish	3	2	2	3	1	3
Shrimps	2	1	0	0	0	0
Amphipods	3	2	0	0	0	0
Gastropods	1	1	0	0	3	10
Estimated wet weight						
Arctic cod	4527	94	1429	94	524	51
Saffron cod	99	2	62	4	0	0
Sculpins	16	<1	8	<1	0	0
Herring	0	0	0	0	500	48
Sand lance	126	3	2	<1	0	0
Unidentified fish	30	<1	20	1	10	1
Shrimps	<1	<1	0	0	0	0
Amphipods	<1	<1	0	0	0	0
Gastropods	1	<1	0	0	3	<1

[a] Values in parentheses are the percentage of all stomachs examined. Remaining percentages are the percent number or weight among birds with identifiable prey remains.

Table 3
Mean (± SE) numbers of fishes in the diets of murres and kittiwakes at Cape Thompson, 1988

Species	Date		
	6–12 July	11 August	27 August
Thick-billed Murre (n)	(19)	(15)	(12)
Arctic cod	6.1 ± 2.0	0.53 ± 0.27	0.17 ± 0.11
Saffron cod	0.21 ± 0.12	0	0
Sand lance	0	0	1.5 ± 0.71
All fish	6.3 ± 1.2	0.73 ± 0.28	1.9 ± 0.72
Common Murre (n)	(8)	(6)[a]	
Arctic cod	6.4 ± 0.75	1.2 ± 0.83	
Saffron cod	0.13 ± 0.13	0.17 ± 0.17	
Sand lance	0	0.17 ± 0.17	
All fish	6.5 ± 0.65	2.2 ± 0.79	
Black-legged Kittiwake (n)	(12)	(6)[a]	
Arctic cod	1.4 ± 0.47	0.83 ± 0.54	
Herring	0.33 ± 0.14	0.17 ± 0.17	
All fish	1.8 ± 0.43	1.0 ± 0.52	

[a] Includes one bird collected on 27 August.

Observations from Cape Thompson and at sea indicate that herring have migrated out of the area by late August. Sand lance are a relatively minor component of the fish fauna in August (Alverson and Wilimovsky 1966) but in many years constitute an important part of piscivorous seabird diets (Springer and Roseneau 1978, 1979; Springer et al. 1984). Our observations at sea and from the colony at Cape Thompson, together with the scarcity of sand lance (and capelin) in seabird diets compared with previous years, suggest that sand lance (and capelin) were uncommon in 1988, possibly because the water temperatures were colder than normal (Springer et al. 1984; Piatt 1987).

Pelagic fish were widely dispersed on our surveys in late August. Average densities estimated for inshore (0.73 $g \cdot m^{-3}$) and offshore (0.073 $g \cdot m^{-3}$) areas correspond to fish concentrations of less than about one fish per 100 m^3. Even some of the dense aggregations observed inshore included only about 30–300 fish per 100 m^3. These estimates were corroborated by visual inspection of echogram traces. Owing to higher densities inshore, the total biomass (6200 mt) of fish inshore (in the 1170-km^2 area in which survey No. 11 was conducted) was higher than the total biomass (5080 mt) offshore (in the 2320-km^2 area offshore circumscribed by survey No. 10). Consistent with these observations, Alverson and Wilimovsky (1966) caught fewer Arctic cod (mean ± SE, 58 ± 12, n = 28) during standardized offshore trawls (outside the 30-m contour) than on trawls conducted inshore (217 ± 144, n = 7). As indicated by variance/mean ratios (I') calculated for those trawls, Arctic cod were more highly aggregated inshore (I' = 669) than offshore (I' = 76).

Thus, it appears that, in August, fish were more abundant and tended to aggregate more in Coastal waters than in offshore Bering/Anadyr waters. As indicated by the negative correlation with SST gradients on the surveys over the front, fish avoided the core of transitional (frontal) waters between the two currents. Furthermore, pelagic fish in stratified Bering/Anadyr waters were concentrated in midwater above the 2°C isotherm, whereas inshore they formed dense concentrations down to the bottom (possibly because bottom water temperatures were much warmer inshore). Fish in Coastal waters also tended to aggregate near the front with Bering/Anadyr water, as indicated by the positive correlation between fish density and SST gradients on the inshore survey.

Table 4
Body weight (g) and mean indices of subcutaneous (Sub-fat) and mesenteric (Mes-fat) body fat content of Thick-billed Murres (TBMU), Common Murres (COMU), and Black-legged Kittiwakes (BLKI) collected at Cape Thompson

Species	Date	Male + female			Male			Female			Sub-fat		Mes-fat	
		Wt.	SE	n	Wt.	SE	n	Wt.	SE	n	Mean	SE	Mean	SE
TBMU	6–8 Jul.	1037	15	19	1051	16	16	963	14	3	1.5	0.1	0.9	0.1
TBMU	11 Aug.	952	15	15	972	18	9	921	21	6	2.2	0.1	1.3	0.1
TBMU	27 Aug.	946	15	12	949	22	8	941	9	4	2.1	0.2	1.3	0.1
COMU	8 Jul.	1030	24	8	1007	28	3	1044	32	5	2.0	0.0	1.0	0.0
COMU	11 Aug.[a]	985	28	6	990	55	3	980		3	2.2	0.2	1.0	0.0
BLKI	8–12 Aug.	508	18	11	545	20	6	452	18	6	2.3	0.2	2.1	0.2
BLKI	11 Aug.	485	16	4	485	16	4	—	—	—	1.4	0.2	1.6	0.2
Overall means[b]														
TBMU		985	11	46	1005	13	33	937	12	13				
COMU		1011	19	14	998	31	6	1020	23	8				
BLKI		495	15	16	521	16	10	452	18	6				

[a] Includes one bird collected on 27 August.

[b] Thick-billed Murre males significantly heavier than females on 6–8 July ($t = 4.14$, $df = 17$, $P < 0.01$) and over all dates combined ($t = 3.84$, $df = 44$, $P < 0.01$). Male kittiwakes heavier than females ($t = 3.46$, $df = 10$, $P < 0.01$). Male Thick-billed Murres ($t = 4.3$, $df = 23$, $P < 0.001$) and kittiwakes ($t = 2.34$, $df = 8$, $P < 0.05$) significantly lighter between July and August. Significant increase in fat content of Thick-billed Murres (Sub-fat: $t = 4.95$, $df = 32$, $P < 0.001$; Mes-fat: $t = 2.83$, $df = 32$, $P < 0.001$) and decrease in fat content of kittiwakes (Sub-fat: $t = 3.18$, $df = 15$, $P < 0.01$; Mes-fat: $t = 1.76$, $df = 15$, $P > 0.05$) between July and August. All other comparisons nonsignificant using two-tailed t-test.

4.2. Foraging ecology and distribution of seabirds

As previous investigators (Swartz 1967; Divoky 1978; Drury et al. 1981) have done, we found that murres, shearwaters, and kittiwakes were the most abundant and widely distributed seabirds in the southeastern Chukchi Sea in late summer. Swartz (1966, 1967) and Springer et al. (1984) noted the importance of the Bering Sea and Alaska Coastal currents, and the front between them, in determining the distribution of seabirds. On the basis of those studies and our own findings, we have reached the following conclusions about seabird foraging ecology in the southeastern Chukchi Sea.

All of the dominant seabirds breeding at Cape Thompson are piscivorous, and most were found within coastal waters where fish densities were highest. Their relative distribution between Alaska Coastal, transitional, and Bering Sea waters was consistent with the known dietary habits of each species. Murre numbers were positively correlated with fish densities. Common Murres feed almost exclusively on dense schools of pelagic fish (Springer et al. 1984; Piatt et al. 1988; Piatt 1990), and they showed a greater affinity for Alaska Coastal water than any other species. Thick-billed Murres also feed heavily on fish but generally have a more diverse diet than Common Murres (Springer et al. 1984; Piatt et al. 1988). Accordingly, a higher proportion of Thick-billed Murres foraged in transitional and Bering Sea waters compared with Common Murres. Transitional waters could possibly have a greater diversity of prey types than adjacent Bering Sea or Coastal waters, because both water masses and associated prey contribute to the composition of transitional waters. Furthermore, upwelling or downwelling at the front may serve to bring prey to the surface or concentrate prey in surface slicks (Brown 1980; Brown and Gaskin 1988; Schneider et al. 1990). Similarly, Horned Puffins, kittiwakes, and Glaucous Gulls, which feed heavily on pelagic fish but also have more diverse diets than Common Murres (Swartz 1966; Springer et al. 1984), were more often found in transitional and Bering Sea waters.

Five other common seabirds that did not breed in the Cape Thompson area were observed on our surveys. Least Auklets foraged widely over stratified Bering Sea waters and were concentrated on the Bering Sea side of the front off Cape Thompson. Least Auklets have a strong preference for Bering Sea/Anadyr copepods (e.g., *Neocalanus plumchrus*) (Bédard 1969; Hunt et al. 1990), and zooplankton are much more abundant in Bering Sea waters off Cape Thompson than in adjacent Coastal waters (English 1966). Vertical stratification and upwelling may be important mechanisms for concentrating zooplankton exploited by Least Auklets (Hunt et al. 1990). Parakeet Auklets have more diverse diets than Least Auklets (Bédard 1969), and they were more widely distributed among water types. Short-tailed Shearwaters and Tufted Puffins feed on a variety of prey, including fishes, euphausiids, shrimp, squid, and other invertebrates (Hunt et al. 1981), and shearwaters exhibited a stronger affinity for transitional waters than other species. Shearwaters (including Sooty Shearwater *Puffinus griseus*) are often associated with fronts (Schneider 1982; Briggs et al. 1987). Phalaropes (of which 91% were identified as Red Phalaropes) were one of the most abundant seabirds we encountered, and most were found on the Alaska Coastal side of the front north of Point Hope. Phalaropes forage on planktonic prey that accumulate in surface slicks near convergent fronts (Brown and Gaskin 1988).

4.3. Foraging and breeding success of seabirds at Cape Thompson

Perhaps the most interesting question to be asked about the fish densities we observed is: Were they sufficient to support seabirds at the end of their breeding season at Cape Thompson in 1988? Forage fish densities near seabird colonies typically vary a lot during the course of summer, usually reaching a peak during midsummer when chicks are hatching and declining towards the end of the breeding period (Safina and Burger 1985; Piatt 1987, 1990). Except for a few schools found inshore, where densities reached 10–100s $g \cdot m^{-3}$, fish densities were low (0.1–10s $g \cdot m^{-3}$) in late August throughout the study area and especially near Cape Thompson. Fish densities were undoubtedly much higher in July when Arctic cod form large, dense schools along the retreating ice edge and nearshore (Lowry and Frost 1981; Springer et al. 1984; Bradstreet et al. 1986). Accordingly, the frequency of cod in murre and kittiwake stomachs at Cape Thompson declined by about an order of magnitude between July and August. Although a decline in fish availability at the end of the breeding season may be a normal experience for seabirds at Cape Thompson (and elsewhere), the frequency of fish in murre and kittiwake stomachs in August 1988 was much lower than in several previous years of study (Springer et al. 1984).

Murres and kittiwakes were affected differently by the low forage fish densities we observed in August 1988. Although murres lost weight between July and August, their body fat stores remained stable or increased, and their breeding success (approximately 50%: BSF, unpubl. data) was normal for these species in Alaska (Piatt et al. 1988). In contrast, kittiwakes lost weight and fat stores in August and experienced the second lowest level of breeding success (about 12%: BSF, unpubl. data) recorded for Cape Thompson in eight years. The marked difference between murres and kittiwakes in body condition and breeding success may have resulted from both the inability of surface-feeding kittiwakes to exploit forage fish below the ocean surface and the scarcity of sand lance, which often comprise the bulk of kittiwake diets in August (Springer et al. 1984). Cold water temperatures probably inhibit the northward migration of sand lance to Cape Thompson (Springer et al. 1984), and that may have accounted for their scarcity in 1988.

5. Summary

As in other oceanic regions (Brown 1980; Schneider 1982; Haney 1986; Briggs et al. 1987), we found that seabird foraging habitats in the southeastern Chukchi Sea were delineated by oceanographic features that could be characterized by gradients in water temperature and salinity. Forage fish school density, abundance, and distribution (vertical and horizontal) varied considerably between habitats. These variations appeared to determine where some seabird species foraged and influenced their foraging and breeding success.

The use of hydroacoustics to study seabird prey below the ocean surface offers great promise for helping to define marine habitats, for studying ecological segregation of seabirds at sea, and for bridging the gap in knowledge between the biology of seabirds at their colonies and at sea. This is particularly true for Arctic and sub-Arctic waters where subsurface foragers dominate seabird communities and pelagic prey are easily detected.

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Appendix 1
Species and numbers of marine birds and mammals observed on all surveys in the southeastern Chukchi Sea (in order of abundance)[a]

Common name	Scientific name	No.
Murre spp.		8237
Thick-billed Murre	*Uria lomvia*	680
Common Murre	*Uria aalge*	198
Short-tailed Shearwater	*Puffinus tenuirostris*	1292
Black-legged Kittiwake	*Rissa tridactyla*	684
Eider spp.		647
King Eider	*Somateria spectabilis*	2
Phalarope spp.		271
Red Phalarope	*Phalaropus fulicaria*	91
Red-necked Phalarope	*Phalaropus lobatus*	8
Least Auklet	*Aethia pusilla*	165
Glaucous Gull	*Larus hyperboreus*	131
Horned Puffin	*Fratercula corniculata*	101
Parakeet Auklet	*Cyclorrhynchus psittacula*	76
Tufted Puffin	*Fratercula cirrhata*	23
Brant	*Branta bernicla*	20
Northern Fulmar	*Fulmarus glacialis*	14
Jaeger spp.		15
Pomarine Jaeger	*Stercorarius pomarinus*	11
Parasitic Jaeger	*Stercorarius parasiticus*	3
Arctic Tern	*Sterna paradisaea*	9
Pacific Loon	*Gavia pacifica*	3
Oldsquaw	*Clangula hyemalis*	2
Sabine's Gull	*Xema sabini*	2
Herring Gull	*Larus argentatus*	2
Crested Auklet	*Aethia cristatella*	2
Common Loon	*Gavia immer*	1
Pelagic Cormorant	*Phalacrocorax pelagicus*	1
Pigeon Guillemot	*Cepphus columba*	1
Gray Whale	*Eschrichtius gibbosus*	24
Humpback Whale	*Megaptera novaeangliae*	1
Spotted Seal	*Phoca largha*	1

[a] For survey effort, see Table 1.

Spatial covariance in counts of birds at sea off eastern Newfoundland

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Abstract

Most marine organisms exhibit some degree of spatial covariance in abundance; in other words, high (or low) densities tend to occur in proximity rather than at random. Models of spatial association can be used to remove the distorting effects of autocorrelation on confirmatory analyses, such as tests for significant change in abundance, habitat usage, or energy turnover by marine bird populations. The purpose of this paper was to determine the strength of autocorrelation of marine bird counts along extended transects at sea and whether spatial association can be described by either autoregressive or moving-average models. We analyzed data for Atlantic Puffins *Fratercula arctica*, murres (primarily Common Murres *Uria aalge*), Northern Fulmars *Fulmarus glacialis*, Black-legged Kittiwakes *Rissa tridactyla*, and Greater Shearwaters *Puffinus gravis* along 15 transects near the eastern coast of Newfoundland in 1985 and 1987. Transects were divided into equal segments (or bins) of 300, 600, and 1200 m in order to compute autocorrelation among the number of sightings per bin. Significant autocorrelation (at $P \leq 0.05$) was observed for all five taxa, along all transects where each taxon was present. We used the sample autocorrelation function (SACF) and the sample partial autocorrelation function (SPACF) to diagnose the spatial association as representative of either an autoregressive (AR) or moving-average (MA) process. The single-parameter moving-average model, or MA(1), was most common. Parameter estimates ranged from 0.46 to 0.98: 75% of 72 cases could best be described by an MA(1) model, 4% could best be described by an AR model, and 21% could not be described as wholly one or the other. These results can be used to investigate changes in abundance of, or in the localization of energy turnover by, birds at sea.

Résumé

L'abondance de la plupart des organismes marins présente un certain degré de covariance spatiale; autrement dit, les zones de densité élevée (ou faible) ont tendance à être davantage groupées qu'aléatoires. Il est possible de recourir à des modèles d'association spatiale pour éliminer les effets de distorsion de l'autocorrélation sur les analyses confirmatoires, comme les tests de détermination des changements significatifs de l'abondance, de l'utilisation des habitats ou du renouvellement de l'énergie pour des populations d'oiseaux marins. L'objectif de l'étude était 1) de déterminer le degré d'autocorrélation des nombres d'oiseaux marins comptés sur de longs transects en mer; et 2) d'établir s'il est possible de décrire l'association spatiale par des modèles autorégressifs ou de moyennes mobiles. Nous avons analysé les données obtenues pour le Macareux moine *Fratercula arctica*, les marmettes (principalement la Marmette de Troïl *Uria aalge*), le Fulmar boréal *Fulmarus glacialis*, la Mouette tridactyle *Rissa tridactyla*, et le Puffin majeur *Puffinus gravis*, sur 15 transects près de la côte est de Terre-Neuve en 1985 et 1987. Les transects ont été divisés en segments égaux (ou compartiments) de 300, 600, et 1200 m afin de calculer l'autocorrélation pour le nombre d'observations par compartiment. Une autocorrélation significative ($P \leq 0{,}05$) a été observée pour les cinq taxons, et ce pour tous les transects où chaque espèce était présente. Nous avons utilisé les fonctions d'autocorrélation et d'autocorrélation partielle pour établir si l'association spatiale est représentative d'un processus autorégressif ou d'un processus de moyennes mobiles. Le modèle à moyennes mobiles à un seul paramètre était le plus commun. Les estimations du paramètre variaient de 0,46 à 0,98 : sur 72 cas examinés, la meilleure description était fournie par ce modèle dans 75 % des cas et par un modèle autorégressif dans 4 % des cas; 21 % des cas n'ont pu être décrits entièrement par l'un ou l'autre des modèles. Ces résultats peuvent être utilisés pour étudier les changements relatifs à l'abondance des oiseaux en mer ou à la localisation du renouvellement de l'énergie par ces oiseaux.

1. Introduction

The distribution of birds at sea exhibits spatial structure at scales ranging from metres to thousands of kilometres. At least two different mechanisms have been proposed to explain spatial structure at the scale of metres to tens of kilometres. One, a relatively fine-scale mechanism operating at scales limited by avian vision, is that birds aggregate in the vicinity of other feeding animals (e.g., Hoffman et al. 1981; Evans 1982). A second mechanism, operating at scales of tens of metres (e.g., Brown and Gaskin 1988) to tens of kilometres (Schneider 1982; Haney and McGillivary 1985), is that foraging birds collect at physical features that concentrate prey. Activities other than feeding, such as movements constrained by wind directions and coastal configuration during the passage of storms (Blomqvist and Peterz 1984), are also important sources of spatial structure in marine birds.

Spatial autocorrelation, regardless of the mechanism causing it, raises the problem of detecting significant change in abundance from place to place or from time to

time. Counts that are not independent preclude the use of simple statistical criteria based on degrees of freedom determined from the number of counts. In practical contexts, such as monitoring change in abundance or detecting change in abundance relative to an event such as an oil spill, autocorrelation cannot be ignored if statistical methods are to be used.

One solution is to design a censusing program to achieve independent counts, using techniques such as random placement of counts at spatial separations greater than the scale of autocorrelation. In the ocean, where travel between points by ship or aircraft is expensive and time-consuming, this solution greatly increases the costs of information by increasing the amount of time spent moving between points relative to time spent collecting data.

A second solution is to estimate and then remove the effect of autocorrelation through regression. This allows more information to be gathered per hour at sea. If counts are autocorrelated, and if a suitable model of autocorrelation can be identified, then the effects of autocorrelation can be removed from the data by applying regression techniques. The residual variation, free of autocorrelation, can be used to test for effects of primary concern, such as change in mean abundance.

The degree of autocorrelation in counts of marine birds has rarely been estimated. In a review of methods, Schneider (1990) analyzed counts along a single transect running through Gray Strait into Hudson Strait. Autocorrelation was significant in Black-legged Kittiwakes *Rissa tridactyla* and Northern Fulmars *Fulmarus glacialis* along this transect, both in the air and on the water. Correlations (Pearson r) exceeded 0.4 in some cases. It is not known whether these results are typical or unusual, because only a single transect was analyzed. The purpose of this paper is to determine the strength of autocorrelation of marine birds along several transects in the Labrador Current and the consistency with which spatial autocorrelation can be described by using autoregressive and moving-average models (Box and Jenkins 1976; Abraham and Ledolter 1983).

2. Autoregressive integrated moving-average (ARIMA) models

The models considered belong to the autoregressive (AR) and moving-average (MA) families. All of these models are included in the larger class of autoregressive integrated moving-average (ARIMA) models. The MA(1) model can be written:

$$y_t - \mu = -\sum_{i \geq 1} \theta^i (y_{t-i} - \mu) + a_t \qquad (1)$$

where y_t = observations at equally spaced points t
μ = the arithmetic mean of the series
θ = the moving-average parameter
a_t = independent normal errors with mean 0 and variance σ^2.

In higher-order MA models, the weights given to previous observations are a decaying function of more parameters. The MA(1) model is usually written:

$$y_t - \mu = a_t - \theta\, a_{t-1} \qquad (2)$$

The two forms are equivalent (Abraham and Ledolter 1983: p. 215). Equation (1) facilitates comparison with AR models.

The AR(1) model can be written:

$$y_t - \mu = \phi\,(y_{t-1} - \mu) + a_t \qquad (3)$$

where the notation is the same as for the MA(1) model except for the autoregressive parameter ϕ. Higher-order AR models include additional (prior) observations to make their predictions, with a corresponding number of additional parameters to weight them.

When applied to spatial data, MA and AR models predict an observation from previous observations along a transect. With an MA model, the next observation is a function of all previous observations, weighted with decreasing influence at increasing separation. One-parameter MA(1), two-parameter MA(2), and higher-order models are possible. With an AR model, each observation is a function of a fixed number of previous observations — AR(1) of the last observation only, AR(2) of the last two observations only, etc.

AR and MA models are readily distinguished by their autocorrelation and partial autocorrelation functions. The autocorrelation function (ACF) gives the correlation ρ_k for lags indexed by k, which takes on values from 1 to n. The partial autocorrelation function (PACF) gives the partial autocorrelations γ_k for lags k = 1 to n.

For the MA(1) model with parameter θ, the correlation among observations k time points apart is:

$$\rho_1 = -\theta / (1 + \theta^2)$$
$$\rho_k = 0 \text{ for } k > 1 \qquad (4)$$

with partial autocorrelations:

$$\gamma_k = -\theta^k(1 - \theta^2)/(1 - \theta^{2(k+1)}) \text{ for } k > 0 \qquad (5)$$

Figure 1 shows the theoretical ACF and PACF for an MA(1).

Assuming θ is positive, the sample autocorrelation function (SACF) will have a "spike" at lag 1 with random noise thereafter; the sample partial autocorrelation function (SPACF) will have the same large value at lag 1 with a gradual decay thereafter. For an MA(q) model, the SACF will consist of spikes at lags 1 to q and random noise thereafter; the SPACF will remain similar to that of the MA(1).

For an AR(1) model with parameter ϕ, the appearances of the ACF and PACF of the MA(1) are reversed. For the AR(1), we have:

$$\rho_k = \phi^k \text{ for } k > 0 \qquad (6)$$

with partial autocorrelations:

$$\gamma_1 = \phi$$
$$\gamma_k = 0 \text{ for } k > 1 \qquad (7)$$

Figure 2 shows the theoretical ACF and PACF for an AR(1) process.

The SPACF will show a spike at lag 1 with random noise thereafter, and the SACF will show an equal spike at lag 1 with gradual decay thereafter. For an AR(p) process (p > 1), the SPACF will show spikes at lags 1 to p with random noise everywhere else, and the SACF will remain similar to that of the AR(1).

Figure 1
Autocorrelation function (ACF) and partial autocorrelation function (PACF) for MA(1) model with parameter 0.8

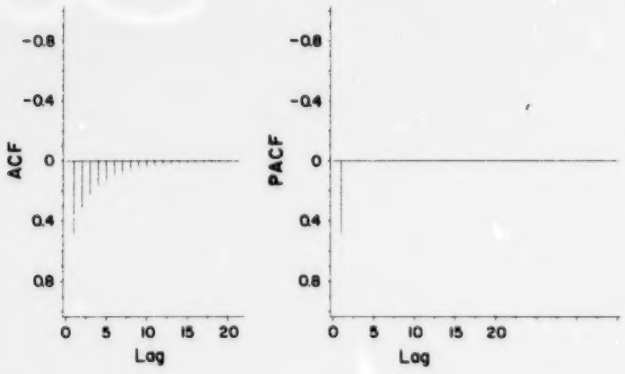
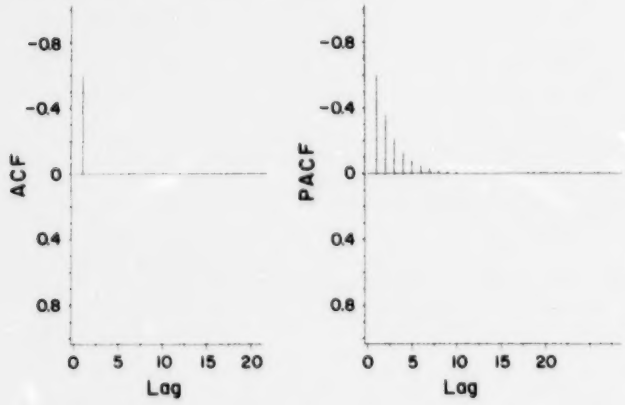


Figure 2
ACF and PACF for AR(1) model with parameter 0.6



3. Field methods

Counts of marine birds were recorded in strips of fixed width: 100, 200, or 300 m during any single traverse, depending on visibility. All birds seen within the strip on one side of the ship were recorded; ship-following birds were noted and excluded from counts. Ship speeds were 4 knots (2 $m \cdot s^{-1}$) or greater. Polling frequency was either once per minute, using pencil and watch, or twice per second, using a program in BASIC running on a Radio Shack 100 laptop computer with internal clock. Recording of data to internal memory lagged up to 3 s behind data entry because of slow response of the screen display in the BASIC program. Minimum resolution was therefore set at 5 s for counts with the computer.

In total, 190 traverses (passage along a transect from start to stop time) were completed in the Labrador Current between Hudson Strait and Nova Scotia (Fig. 3), from June 1985 through December 1987. Several traverses were repeats of the same transect. We restricted our analyses to those traverses greater than 31.2 km. This assured at least 26 contiguous segments (bins) of 1200 m each, the largest bin size that we used. Most traverses were made on an opportunistic basis, during oceanographic cruises aboard vessels from the Bedford Institute of Oceanography (BIO)

Figure 3
Location of transects in the southern Labrador Current

(Dartmouth, N.S.). A few traverses (July 1985) were made along directed transects aboard either a sailing vessel or BIO ship (Schneider et al. 1990).

A case was defined as the record of the location of all birds of a single taxon (species, except for murres *Uria*) along a single traverse. We analyzed only those cases in which at least 50 birds of a taxon were seen along a traverse. Counts were tabulated in contiguous bins of fixed length, either 300, 600, or 1200 m. Ship speed was used to calculate time periods corresponding to bin lengths.

Standard methods of estimation and hypothesis testing (Box and Jenkins 1976) require that the series of observations be stationary, that is, have a constant mean and constant variance–covariance structure. In particular, the lagged autocorrelations can depend only on the distance between observations, and not upon the time (or location) itself. The variance of the bird counts tended to increase with their magnitude, so data were transformed to a logarithmic scale to remove this effect. The observations also tended to increase or decrease systematically over the course of a traverse. This effect was removed by taking the difference between successive (log-transformed) counts, producing data that fluctuated with consistent variability around a fixed mean. These derived values can be interpreted as the ratios of counts in successive bins. Results pertain to the derived values, unless stated otherwise. All calculations were made with the BMDP package (Dixon 1983).

The sample autocorrelation coefficients were calculated at lags 1 and higher. Lag 1 correlations typically exceeded correlations at higher lags, so we report only lag 1

Table 1
Date, starting time, duration, length, and location of transects (TR) A through O in coastal waters of Newfoundland (S = start, E = end)

TR	Date	Starting time (GMT)	Duration (min)	Length (km)	Location °N latitude	°W longitude	
1985							
A	28 Jun.	1235	215	45.3	46 39.1′	54 19.8′	S
					46 36′	53 53′	E
B	24 Jul.	1235	360	76.3	47 29′	52 36.5′	S
					46 51′	52 52′	E
C	25 Jul.	805	345	71.1	46 39.3′	51 59.5′	S
					47 15′	52 46.2′	E
D	25 Jul.	1735	275	56.6	47 16.2′	52 46.1′	S
					47 19′	52 00′	E
E	5 Aug.	1130	191	79.9	46 42′	52 06′	S
					47 15.7′	52 45.5′	E
F	8 Aug.	1530	264	88.4	50 15.9′	54 55.3′	S
					50 26.9′	56 05′	E
G	11 Aug.	1050	126	51.9	48 29.5′	52 45′	S
					48 10′	53 15.5′	E
H	11 Aug.	1256	274	35.1	48 10′	53 15.5′	S
					47 53.6′	53 29.7′	E
I	4 Sept.	1500	90	35.7	50 23.2′	53 17.4′	S
					50 39.6′	53 33.4′	E
J	8 Sept.	950	205	69.0	54 32.3′	53 55.5′	S
					54 29.5′	54 59.5′	E
K	8 Sept.	1735	120	38.3	54 29.1′	55 45.3′	S
					54 28.6′	56 20.8′	E
L	18 Sept.	1311	89	42.9	60 30.8′	64 26.9′	S
					60 29.8′	65 13.9′	E
1987							
M	24 May	805	150	45.2	48 40′	52 41′	S
					48 48′	53 16′	E
N	24 May	1438	120	41.5	49 19.4′	53 05′	S
					49 40.5′	52 53′	E
O	26 May	1500	150	48.2	49 42′	55 44′	S
					49 57′	55 11.5′	E

correlations, with their standard errors, for each case of more than 50 birds of one species along a single traverse.

The SACF and SPACF were computed and then compared, in order to choose an appropriate model of autocorrelation within a traverse. We chose a moving-average model if the SACF showed a spike while the SPACF showed decay with increasing lag, as in Figure 1. We chose an autoregressive model if the SACF showed decay with increasing lag while the SPACF showed a spike, as in Figure 2. Once an AR or MA form had been chosen, a one-parameter model was fitted, and the residuals from the model were examined for significant autocorrelation. The criterion for significance was 5% in this and all other tests. If fewer than four of the first 20 autocorrelations (partial or simple) of the residuals were significant, a one-parameter model was chosen. If four or more significant autocorrelations were present, a more complex model was tried. If the appropriate model was not identifiable as wholly MA or AR, we simply reported this result rather than trying to fit a complex model.

4. Results

Fifteen transects proved long enough (31.2 km) for analysis (Table 1). Figure 3 shows the location of each transect. We obtained 22 cases in which at least 50 birds of a single taxon were recorded along a traverse: seven for Northern Fulmar (Table 2), three for Greater Shearwater *Puffinus gravis* (Table 3), three for Black-legged Kittiwakes (Table 4), three for murres (Table 5), and six for Atlantic Puffins *Fratercula arctica* (Table 6). In addition, we

Table 2
Spatial autocorrelation in the first differences of log-transformed counts of Northern Fulmars along seven transects (TR), as in Table 1[a]

TR	Bin size (m)	n	$\rho_1 \pm$ SE	Model	$\theta \pm$ SE	Residual
F	300	298	−0.56 ± 0.06	MA(1)	0.93 ± 0.020	
	600	148	−0.54 ± 0.08	MA(1)	0.85 ± 0.044	10
	1200	73	−0.47 ± 0.12	MA(1)	0.78 ± 0.073	
I	300	120	−0.34 ± 0.09	—	NA	NA
	600	60	−0.53 ± 0.13	—	NA	NA
	1200	29	−0.37 ± 0.19	—	NA	NA
J	300	232	−0.48 ± 0.07	MA(1)	0.91 ± 0.025	
	600	114	−0.58 ± 0.09	MA(1)	0.88 ± 0.045	17
	1200	57	−0.21 ± 0.13	—	NA	NA
K	300	128	−0.43 ± 0.09	MA(1)	0.98 ± 0.005	8
	600	64	−0.63 ± 0.13	—	NA	NA
	1200	32	−0.63 ± 0.18	—	NA	NA
L	300	144	−0.49 ± 0.08	MA(1)	0.65 ± 0.063	
	600	72	−0.11 ± 0.12	MA(1)	0.46 ± 0.105	
	1200	35	−0.15 ± 0.17	—	NA	NA
N	300	136	−0.48 ± 0.09	MA(1)	0.95 ± 0.025	18
	600	68	−0.55 ± 0.12	MA(1)	0.90 ± 0.051	10
	1200	34	−0.54 ± 0.17	MA(1)	0.89 ± 0.076	5
O	300	158	−0.49 ± 0.08	MA(1)	0.96 ± 0.018	
	600	78	−0.19 ± 0.11	MA(1)	0.89 ± 0.051	
	1200	39	−0.16 ± 0.16	MA(1)	0.80 ± 0.101	

[a] n = number of bins. ρ_1 is simple autocorrelation at lag 1. MA(1) = one-parameter moving-average model, AR = autoregressive model, — = not wholly MA or AR. θ = MA(1) parameter. NA = not applicable. Significant residual autocorrelation (at P = 0.05) noted and listed by lag.

Table 3
Spatial autocorrelation in the first differences of log-transformed counts of Greater Shearwaters along three transects[a]

TR	Bin size (m)	n	$\rho_1 \pm$ SE	Model	$\theta \pm$ SE	Residual
A	300	151	−0.54 ± 0.08	—	NA	NA
	600	75	−0.47 ± 0.12	MA(1)	0.84 ± 0.069	
	1200	37	−0.51 ± 0.16	AR	NA	9
F	300	298	−0.46 ± 0.06	MA(1)	0.93 ± 0.021	
	600	148	−0.50 ± 0.08	MA(1)	0.87 ± 0.038	
	1200	73	−0.32 ± 0.12	—	NA	NA
G	300	175	−0.43 ± 0.08	MA(1)	0.97 ± 0.011	3, 8
	600	86	−0.35 ± 0.11	MA(1)	0.96 ± 0.023	
	1200	43	−0.43 ± 0.15	MA(1)	0.91 ± 0.059	

[a] For explanation of columns, see footnote to Table 2.

analyzed flying murres separately from murres on the water along one traverse (Table 5), for a grand total of 24 cases, each at three different bin sizes.

Figure 4 shows a typical series of counts — all murres sighted along transect D on 25 July 1985. When these raw counts are differenced at lag 1 (count 2 − count 1, count 3 − count 2, etc.), the resulting plot (Fig. 5) shows a pattern of large differences in areas of high counts and low differences in areas of low counts. When the logarithms of the counts were differenced, the result was consistent variation along the entire transect. Plots of the differenced counts and the differenced logarithms are shown in Figure 5.

The lag 1 autocorrelation of the log-transformed and differenced data, over all 72 analyses (Tables 2–6), averaged −0.48, with a range of −0.15 to −0.63. All but two of the 72 coefficients differed significantly from zero (Table 2). Autocorrelation did not differ among species ($F = 0.87$, df = 4 and 67, $P = 0.488$). Nor did autocorrelation differ among bin sizes ($F = 0.40$, df = 2 and 69, $P = 0.671$).

In the majority of cases (54 of 72), an MA(1) model described the autocorrelative structure in the data. The data in Figures 3 and 5 are typical. The SACF (Fig. 6) shows a single high value at lag 1, with much smaller values at

Table 4
Spatial autocorrelation in first differences of log-transformed counts of Black-legged Kittiwakes along three transects[a]

TR	Bin size (m)	n	$\rho_1 \pm$ SE	Model	$\theta \pm$ SE	Residual
B	300	257	−0.57 ± 0.06	MA(1)	0.90 ± 0.026	
	600	127	−0.44 ± 0.09	MA(1)	0.77 ± 0.055	
	1200	63	−0.47 ± 0.13	MA(1)	0.63 ± 0.095	19
H	300	117	−0.47 ± 0.09	MA(1)	0.82 ± 0.049	
	600	58	−0.45 ± 0.13	—	NA	NA
	1200	29	−0.62 ± 0.19	AR	NA	
L	300	144	−0.49 ± 0.08	—	NA	
	600	72	−0.54 ± 0.12	MA(1)	0.77 ± 0.074	5
	1200	35	−0.49 ± 0.17	MA(1)	0.50 ± 0.148	

[a] For explanation of columns, see footnote to Table 2.

Table 5
Spatial autocorrelation in first differences of log-transformed counts of murres along five transects[a]

TR	Bin size (m)	n	$\rho_1 \pm$ SE	Model	$\theta \pm$ SE	Residual
B	300	257	−0.39 ± 0.06	MA(1)	0.90 ± 0.026	2
	600	127	−0.18 ± 0.09	MA(1)	0.87 ± 0.043	6, 18, 20
	1200	63	−0.57 ± 0.13	MA(1)	0.83 ± 0.066	
Flying birds only						
	300	257	−0.42 ± 0.06	MA(1)	0.90 ± 0.026	5, 8
	600	127	−0.51 ± 0.09	MA(1)	0.88 ± 0.040	18
	1200	63	−0.62 ± 0.13	MA(1)	0.85 ± 0.062	
Birds on water only						
	300	257	−0.50 ± 0.06	MA(1)	0.95 ± 0.018	18
	600	127	−0.13 ± 0.09	MA(1)	0.90 ± 0.037	14
	1200	63	−0.36 ± 0.13	—	NA	NA
C	300	237	−0.41 ± 0.06	—	NA	NA
	600	118	−0.15 ± 0.09	—	NA	NA
	1200	59	−0.11 ± 0.13	MA(1)	0.98 ± 0.026	
D	300	191	−0.57 ± 0.07	MA(1)	0.83 ± 0.037	11, 13
	600	97	−0.59 ± 0.10	AR	NA	5
	1200	48	−0.31 ± 0.14	—	NA	NA

[a] For explanation of columns, see footnote to Table 2.

larger lags. The SPACF (Fig. 6) shows smoothly decreasing coefficients from lags 1 to 7. When an MA(1) model was fitted to these data, the parameter for this model was 0.83. Significant autocorrelation of the residuals from this model occurred at lags 11 and 13 (Table 5). Autocorrelated residuals suggest that the model in the preceding column of the table may not fully describe the autocorrelation in the data. However, the number of instances of autocorrelated residuals was not large (36 in Tables 2–6) considering the number of coefficients that were examined — about 40 coefficients in each of 24 cases.

An AR model described the autocorrelative structure of the data once for Greater Shearwaters (Table 3), once for Black-legged Kittiwakes (Table 4), and once for murres (Table 5). In these three cases, nearly all birds were observed in single, isolated segments of the transect. This occurred when bin size nearly matched the horizontal extent of an aggregation, as measured by chord length along a transect running through that aggregation. An AR model did not fit at smaller bin sizes.

5. Discussion

A previous analysis showed that counts of both Black-legged Kittiwakes and Northern Fulmars were autocorrelated at lags (distances) of the order of 100–300 m, and of the order of 1 km along a transect through Gray Strait into Hudson Strait (Schneider 1990). The magnitude of spatial autocorrelation, as measured by the absolute value of the simple lag 1 autocorrelation coefficients, was

Table 6
Spatial autocorrelation in first differences of log-transformed counts of Atlantic Puffins along five transects[a]

TR	Bin size (m)	n	$\rho_1 \pm$ SE	Model	$\theta \pm$ SE	Residual
B	300	257	−0.50 ± 0.06	MA(1)	0.92 ± 0.023	6
	600	127	−0.18 ± 0.09	MA(1)	0.87 ± 0.042	
	1200	63	−0.47 ± 0.13	MA(1)	0.87 ± 0.061	
C	300	237	−0.48 ± 0.06	MA(1)	0.88 ± 0.030	17
	600	118	−0.41 ± 0.09	MA(1)	0.78 ± 0.054	8, 11
	1200	59	−0.49 ± 0.13	MA(1)	0.62 ± 0.094	
D	300	194	−0.44 ± 0.07	MA(1)	0.85 ± 0.035	16
	600	97	−0.37 ± 0.10	MA(1)	0.84 ± 0.050	
	1200	48	−0.53 ± 0.14	MA(1)	0.78 ± 0.082	7
E	300	266	−0.51 ± 0.06	MA(1)	0.93 ± 0.027	18
	600	133	−0.55 ± 0.09	MA(1)	0.93 ± 0.036	
	1200	66	−0.56 ± 0.12	MA(1)	0.84 ± 0.070	6
H	300	117	−0.50 ± 0.09	MA(1)	0.90 ± 0.039	10, 16
	600	58	−0.59 ± 0.13	MA(1)	0.88 ± 0.065	17
	1200	29	−0.56 ± 0.19	MA(1)	0.75 ± 0.137	
M	300	152	−0.50 ± 0.08	MA(1)	0.93 ± 0.027	3, 6
	600	75	−0.46 ± 0.12	MA(1)	0.88 ± 0.050	
	1200	37	−0.63 ± 0.16	MA(1)	0.87 ± 0.080	

[a] For explanation of columns, see footnote to Table 2.

similar in the count data (Schneider 1990) and the transformed and differenced data from the same transect (Tables 2–4, transect L). Hence, the significant autocorrelation that we report here cannot be attributed to the transformation and differencing operations required to achieve stationarity.

The observed autocorrelations led us to consider procedures to reduce this problem. Assuming data correspond to a continuous transect (i.e., not randomly spaced points), we may try to reduce autocorrelation in the observed counts either by decimating the series or by pooling counts to create larger units that might have fewer autocorrelated counts.

The expectation behind decimation is that autocorrelation will be reduced by increasing the distance between counts. An example would be the exclusion of every other count in a series. This results in two series, each with half the number of observations. This strategy will effectively reduce the autocorrelation within a series following an AR(1) process, in which counts are a function of one adjacent (previous) count. This strategy will be less effective within a series following an MA process, in which counts are a function of several prior counts. In our analyses, we found that almost all series suggested an MA process. Hence, decimation cannot be relied upon to eliminate autocorrelation of counts along transects.

A second method for eliminating autocorrelation is to pool small-scale counts into larger-scale counts, such as pooling of 300-m counts into 1200-m counts. Suppose that new observations are formed by partitioning counts into pairs and then pooling the observations within each pair. For example:

$$'c_1 = c_1 + c_2$$
$$'c_2 = c_3 + c_4 \qquad (8)$$

This doubles the bin size used in analysis. We can, in a similar fashion, pool sets into triplets, quadruplets, or larger groupings, because there is no natural segment length with which to work. Pooling will reduce autocorrelation if the covariances among successive observations increase less rapidly than the variance. However, the adjustment of segment length may also encompass larger-scale processes leading to increasing covariance, so we have no guarantee that pooling will decrease autocorrelation. We found, in fact, that pooling

Figure 4
Murres, primarily Common Murres *Uria aalge* (flying and on water), sighted along transect D, 25 July 1985. Transect runs from breeding colony at Witless Bay eastward across the Avalon channel. Counts are in bin sizes of 300 m.

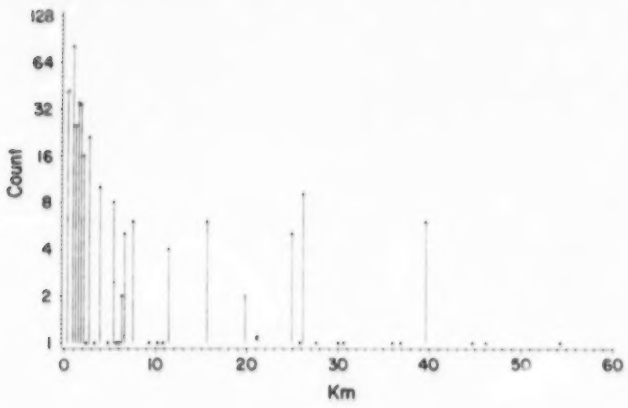
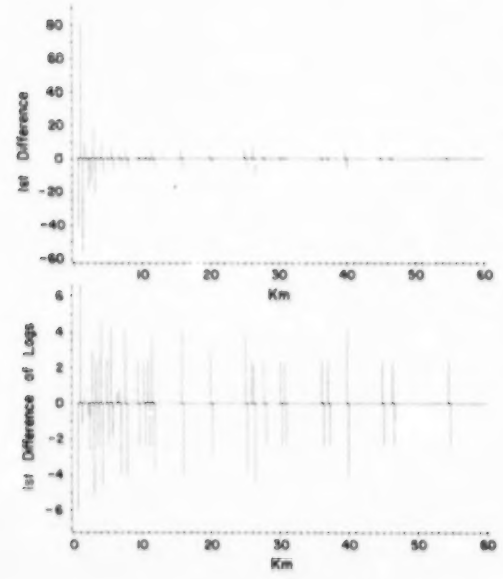


Figure 5
First difference of counts along transect D (top); first difference of log-transformed counts along transect D (bottom)

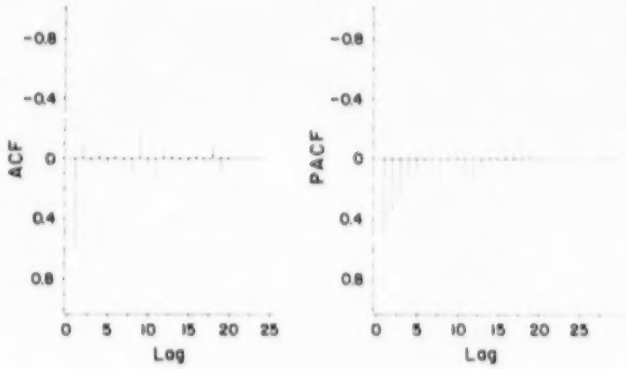


did not reduce autocorrelation. The average correlation coefficient, over 24 analyses, was -0.47 at 300-m bin sizes, -0.47 at 600-m bin sizes, and -0.49 at 1200-m bin sizes.

If differenced data are used, then pooling is equivalent to decimating. Pooling of differenced counts into pairs is equivalent to removing every other count. Similarly, pooling into triplets is equivalent to using only counts c_1, c_4, and c_7. Hence, for differenced counts, pooling will be no more effective than decimation at removing autocorrelation.

To recapitulate briefly, we considered two procedures to reduce autocorrelation — decimation (through deletion or intermittent counting) and pooling. Both will work if data show only local association, in which an observation is related to a few nearby observations. We can diagnose this by examining the SACF for decay in magnitude with increasing lag, and we can use the

Figure 6
SACF and SPACF of (log-transformed) data in Figure 5



SACF to estimate the lag needed to eliminate autocorrelative effects through spacing, decimation, or pooling. However, with marine bird data, we found that the SACF does not decay with increasing lag, and that higher-order (larger spatial scale) autocorrelation appears in the data and remains evident after pooling. This conclusion is consistent with what we now know of the distribution of pelagic birds, which is that aggregation occurs at spatial scales ranging from metres to thousands of kilometres (Hunt and Schneider 1987). We also concluded that, for our data, autocorrelation could not be eliminated by manipulation of the autocorrelation structure through decimation or pooling.

Rather than trying to eliminate sample autocorrelation, we can try to incorporate it into a statistical model. If this is successful and uncorrelated residuals result, these residuals can be used to test for effects of interest, such as changes in abundance at key foraging locations. Our results suggest that this route, statistical control, will be more effective than procedures that alter the autocorrelation structure. In 75% of the cases we examined, spatial autocorrelation could be modeled satisfactorily with a relatively simple moving-average model having a single parameter. The residuals from this model were autocorrelated at relatively few lags or showed no autocorrelation at all. Thus, tests based on residuals from a simple model will be less affected by the problem of autocorrelation than tests based on counts directly. This route is also promising because we found that the MA(1) parameter was fairly consistent across a range of species, bin sizes, and transects. Our parameter values provide a benchmark against which to compare estimates of autocorrelation in other species, at other locations. The consistency of our parameter estimates indicates that we could use this information to eliminate autocorrelation from shorter transects, in which too few contiguous counts were available to develop good parameter estimates for that transect. The major disadvantage with these models is that the transformations required to achieve stationarity make interpretation of results difficult.

At the outset of this analysis, we had no reason to expect that MA models would provide better descriptions of the data than AR models. We found that MA(1) models described spatial autocorrelation in five species along most transects. In retrospect, this result is consistent with the experience of pelagic observers; that is, one can develop expectations about the number of birds that will be seen on

the next count, based on what has been seen over the last few counts. This expectation applies to counts ranging in duration from 1 min (about 300 m at 10 knots) to 10 min (about 3 km at 10 knots). The MA model formalizes this expectation. The predominance of MA over AR models in our analysis indicates that, in general, the expected magnitude of the next count will be a weighted function of all previous counts, rather than some multiple of one or two prior counts.

In three of 72 analyses, an AR model described the data better than an MA model. In all three cases, this result was scale-dependent, appearing at one bin size only, never at all three bin sizes used to analyze one species along a transect. The AR model arises when nearly all birds were found in a small number of adjacent counts. That is, bin size nearly equals the horizontal extent of an aggregation. The shift in the SACF and SPACF from an MA pattern to an AR pattern seems to occur at the spatial scale of the aggregation. One could presumably identify the scale at which important aggregative processes were occurring by comparing the form of the SACF and SPACF over a range of bin sizes. However, such a procedure is far more laborious than spectral methods, which provide a graphically more economical method of assessing variability over a range of bin sizes.

One problem with applying time-series analysis to spatial data is that the technique uses a directional sequence, rather than propinquity in two directions, as in spectral methods (Ripley 1981: p. 112). Transects can be surveyed from either direction, unlike a time series. In such a situation, where no natural direction exists, time-series analysis must be considered a convenient tool for removing the effects of autocorrelation, rather than a forecasting method. We note, however, that many large marine organisms search for prey, rather than sitting and waiting for prey to drift past. For mobile foragers, the direction of search can be in only one direction at a time. The predator can know only what it has seen, not what will occur ahead. In such a situation, where a natural direction exists, time-series analysis may provide a useful means of investigating foraging tactics. For example, given a distribution of prey at the surface of the ocean, how should a predator form expectations about the number immediately ahead? Should the predator form expectations on the basis of conditions immediately before (an AR model) or on the basis of some weighting of past conditions (an MA model)? Over what distance should a predator use prior experience to guide expectation and foraging behaviour in a changing environment? These questions have been addressed in the optimal foraging literature (e.g., Stephens and Charnov 1982; Mangel and Clark 1988) by treating spatial variation in food supply as a classification variable rather than a continuous variable. A time-series analysis of prey distribution, using location as a continuous variable, may prove useful in understanding the searching behaviour of large pelagic predators, including commercial fisheries vessels.

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Seabird distribution as related to food webs and the environment: examples from the North Pacific Ocean

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Abstract

Most piscivorous seabirds in the North Pacific Ocean are supported by only a few taxa of prey during the breeding season. Sympatric, congeneric populations of murres and of kittiwakes have dietary and distributional characteristics that are related to particular marine food webs. The food webs, and thus the avifauna, often change over short distances in association with changes in the prevailing physical environment. Rising and falling trends in numbers of murres, kittiwakes, and auklets at certain colonies in Alaska might be related to similar trends in populations of their principal prey and are suggestive of large-scale changes in the marine ecosystem.

Résumé

La plupart des oiseaux de mer piscivores du Pacifique Nord dépendent de quelques espèces seulement de poissons au cours de la saison de reproduction. L'alimentation et la distribution de populations sympatriques et congénères de marmettes *Uria* spp. et de mouettes *Rissa* spp. sont liées à des réseaux trophiques marins particuliers. Les réseaux trophiques, et conséquemment l'avifaune, changent souvent sur de courtes distances en fonction du milieu physique. Les augmentations et baisses des effectifs de certaines colonies de marmettes, de mouettes et d'alques, en Alaska, pourraient refléter les tendances des populations de leurs principales proies et indiquer des changements importants de l'écosystème marin.

1. Introduction

Broad features of the marine environment have been commonly used to explain distributions of many species of seabirds. For example, in the North Atlantic and North Pacific oceans, the different distributions of Common Murres *Uria aalge* and Thick-billed Murres *U. lomvia* are related to patterns of sea surface temperature resulting from large-scale effects of latitude and ocean circulation: Common Murres are usually more abundant in warmer water, whereas Thick-billed Murres are more abundant in colder water (Tuck 1961; Nettleship and Evans 1985). Theories of the mode of speciation of murres (Bédard 1985), anatomical differences between them (Spring 1971), and differences in diet (see reviews by Bradstreet and Brown 1985; Vermeer et al. 1987) suggest that warm and cold oceanic regions contain different communities of organisms and food webs favoured by the two species.

A mosaic of marine habitats with characteristic food webs contributes to complex patterns of seabird distribution in the North Pacific. There are numerous sympatric, congeneric populations (see Sowls et al. 1978; Vermeer et al. 1987), which provide a way to assess degrees of ecological separation of closely related species and are useful in discovering information about the distributions of marine communities and their relationship to the environment. Knowledge of the relative importance of various prey species is necessary for biological modeling and for the conservation of seabirds, whereas knowledge of interannual patterns in productivity and numerical change in seabird populations, particularly in relation to their food webs, can further contribute to an understanding of ecosystem processes and dynamics.

2. Seabird distribution

2.1. Murres

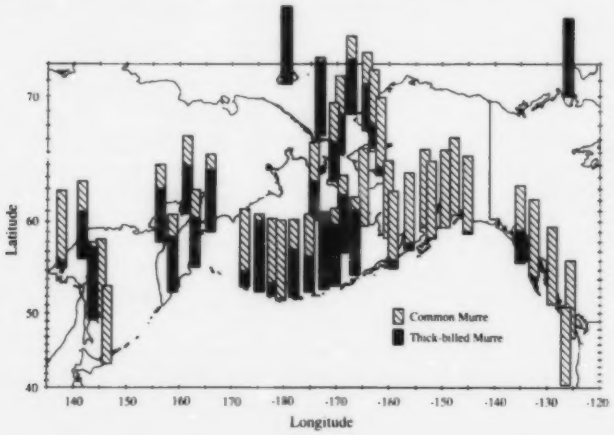
In the eastern North Pacific (Fig. 1), Common Murres far outnumber Thick-billed Murres from California to Bering Strait (Fig. 2). North of Bering Strait, Thick-billed Murres increase in relative number to about 70% of the total at Cape Lisburne in the eastern Chukchi Sea and nearly 100% at Cape Parry in the eastern Beaufort Sea. In the western North Pacific, Common Murres predominate south of the Kamchatka Peninsula but are in the minority to the north, particularly north of Bering Strait. The two species overlap extensively in the Aleutian Islands and on all the offshore islands in the Bering Sea, with large differences in ratios between them at nearby colonies.

The preponderance of Common Murres along the eastern side of the North Pacific is similar to the pattern in the North Atlantic (Fig. 3). Moreover, a warm coastal current flowing out of the Bering Sea ameliorates an otherwise cold environment in the eastern Chukchi Sea (Fig. 4) and extends the range of Common Murres northward just as the Gulf Stream extends their range into the Barents Sea. In contrast, the current flowing northward through western Bering Strait (Fig. 4) is cold and has little effect on the temperature of the cold western Chukchi Sea or the breeding marine avifauna.

Another feature of the eastern North Pacific, where Common Murres predominate, particularly in the Gulf of Alaska and the Bering Sea, is the large extent of continental shelf (Fig. 1). The shelf is much less extensive in the western Bering Sea and is absent along the Aleutian Arc, where Thick-billed Murres tend to be more abundant. The contrast between shelf and oceanic environments has been

Figure 1
Geographic features of the North Pacific Ocean. Depth contours are in metres.

Figure 2
Approximate percentages of Common and Thick-billed murres at colonies in the North Pacific Ocean. See Appendix 1 for sources of data.



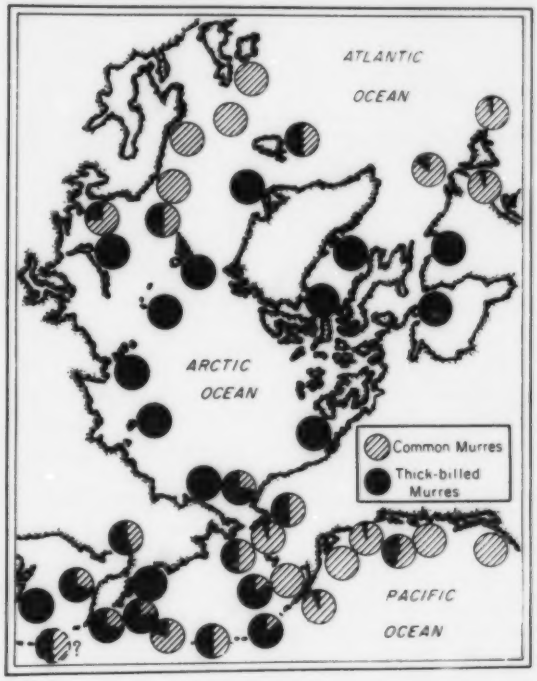
used previously to describe the distributions of murres and other seabirds in the southeastern Bering Sea (Hunt et al. 1981a; Schneider and Hunt 1984; Schneider et al. 1986).

The extensive overlap of Common and Thick-billed murres in the North Pacific contrasts with the situation in the North Atlantic, where both species are abundant but much more segregated (Fig. 3). Where overlap in the North Atlantic does occur, the ratio of Common to Thick-billed murres is usually skewed dramatically in one direction or the other.

2.2. Kittiwakes

Black-legged Kittiwakes *Rissa tridactyla* nest throughout the Bering Sea and Gulf of Alaska at numerous colonies along the mainland coast and on most of the islands. However, Red-legged Kittiwakes *R. brevirostris* nest at only four locations in the world, all of which are near the edge of, or off, the continental shelf (Byrd 1978; Sowls et al. 1978). The nesting distribution of Red-legged Kittiwakes, anatomical differences between them and Black-legged Kittiwakes (e.g., Red-legged Kittiwakes have larger eyes) (Storer 1987), and information on their food habits all indicate that Red-legged Kittiwakes have evolved to exploit nocturnally available prey that are more abundant in the oceanic domain than on the shelf.

Figure 3
Approximate proportions of Common and Thick-billed murres throughout most of their range. See Appendix 1 for sources of data.



3. Major prey

Only a few taxa contribute the bulk of the fish prey consumed by most North Pacific piscivorous seabirds, particularly murres and kittiwakes (Fig. 5) (Hunt et al. 1981b). Cods (Gadidae), sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus*, and herring *Clupea harengus* are the four most important prey, whereas sculpins (Cottidae) are of occasional local importance to Thick-billed Murres, as are flatfishes (Pleuronectidae) to both Thick-billed and Common murres (Appendix 1). This generalization is less appropriate for cormorants (*Phalacrocorax* spp.) and Pigeon Guillemots *Cepphus columba*, which in some locations consume a larger variety of other fishes (Ainley and Sanger 1979; AMS and D.G. Roseneau, unpubl. data).

Three species of cod found in differing environments are regionally of equal importance. Arctic cod *Boreogadus saida* predominate in the Chukchi Sea and the Bering Strait region (e.g., St. Lawrence Island). Arctic cod is the most abundant marine fish in Arctic Alaska (Alverson and Wilimovsky 1966; Quast 1974; Craig et al. 1982) and probably throughout the entire perimeter of the Arctic Ocean, and it is a key species in the ecosystem (Andriyashev 1954; Frost and Lowry 1981; Bradstreet and Cross 1982). Saffron cod *Eleginus gracilis* replaces Arctic cod in the warm, shallow waters of Norton Sound and is important in food webs and energy budgets in that rather small, unique environment (Barton 1977; Wolotira et al. 1979; Frost and Lowry 1981; Springer et al. 1987). Because of the highly advective regime on the Bering–Chukchi shelf (Coachman et al. 1975), saffron cod is also present in the eastern Chukchi Sea but is consumed by seabirds in smaller numbers than Arctic cod (Swartz 1966; Springer et al. 1984). Both of these species are replaced to the south by walleye pollock *Theragra chalcogramma*, the dominant pelagic

Figure 4
Sea surface temperatures on the Bering–Chukchi shelf. NOAA-7 satellite infrared image: warm = darker shading, cold = lighter shading. Warm coastal water flows out of Norton Sound and north into the eastern Chukchi Sea, whereas cold oceanic water from the continental slope flows north through western Bering Strait.

Figure 5
Principal prey of murres, kittiwakes, and most other piscivorous seabirds in the North Pacific and North Atlantic oceans. See Appendix 1 for sources of data.

fish and a key species of the outer shelf and middle shelf domains of the Bering Sea (Iverson et al. 1979; Smith 1981; Springer et al. 1986; Walsh and McRoy 1986; Lowry et al. 1989). It is the most important prey of the majority of piscivorous seabirds nesting on St. Matthew and Hall islands and the Pribilof Islands (Hunt et al. 1981b; Springer et al. 1986).

Cod are generally much less important in diets of piscivorous seabirds nesting along the mainland coast of the southeastern Bering Sea or in the Gulf of Alaska (Fig. 5), except that pollock are common in diets of murres offshore in Bristol Bay (Ogi and Tsujita 1973) and in diets of murres, kittiwakes, Horned Puffins *Fratercula corniculata*, and Tufted Puffins *F. cirrhata* along the south side of the Alaska Peninsula, downstream of a major spawning area of pollock (Megrey 1987). Instead, sand lance and capelin are the principal prey nearshore in the eastern Bering Sea and Gulf of Alaska and are supplemented by herring in Prince William Sound and by Pacific saury *Cololabis saira* in southeastern Alaska.

The diet of Red-legged Kittiwakes is a notable exception to the above generalizations. Red-legged Kittiwakes feed most heavily on lanternfishes (Myctophidae) (Hunt et al. 1981b; AMS et al., unpubl. data), an oceanic taxon that commonly migrates to the surface at night. Red-legged Kittiwakes therefore nest around the perimeter of the Bering Sea basin (Byrd 1978; Sowls et al. 1978) and usually forage at night. Myctophids and squid are the principal prey of many seabirds at Buldir Island in the western Aleutian Islands, and they constitute one of the most extreme departures from the cod–sand lance–capelin pattern known for Alaskan waters.

In the North Atlantic, Arctic cod is perhaps the most important prey of the majority of Thick-billed Murres during summer (Fig. 5). Common Murres, however, by virtue of a very different distribution, probably seldom feed on Arctic cod or other gadids, depending instead on capelin, herring, and sand lance. Considering the physical contrasts between the environments occupied by Common and Thick-billed murres in the North Atlantic, it is not surprising that their diets differ markedly. The preponderance of Common Murres in the cold waters of Newfoundland and Labrador, where relatively more Thick-billed Murres would be expected based on the oceanographic zonation (see Nettleship and Evans 1985), therefore might be a function of the vast capelin stocks in this region of the northwestern Atlantic. The dominant prey species in Newfoundland is capelin, and, perhaps because of competitive exclusion of Thick-billed Murres by Common Murres (e.g., Spring 1971; Williams 1974) or adaptations of Common and Thick-billed murres to exploit different prey, or both, Thick-billed Murres are not numerous.

4. Local examples of habitat–food web relationships

In Alaska, the proportions of the two murre and two kittiwake species can differ markedly at neighbouring colonies. The following cases illustrate how the distributions of marine habitats and associated food webs are related to murre and kittiwake distributions.

4.1. Northern Bering and eastern Chukchi seas

The most striking example in this region is the great preponderance of Common Murres in Norton Sound, whereas approximately 50% of the murres on nearby St. Lawrence Island are Thick-billed Murres. The marine environment around St. Lawrence Island is much more diverse and productive than in Norton Sound because of a current of oceanic water that originates along the continental slope of the Bering Sea and flows north past

Figure 6
Relative numbers of murres and kittiwakes on the Pribilof Islands and the local bathymetry. Numerical data are from Hickey and Craighead (1977).

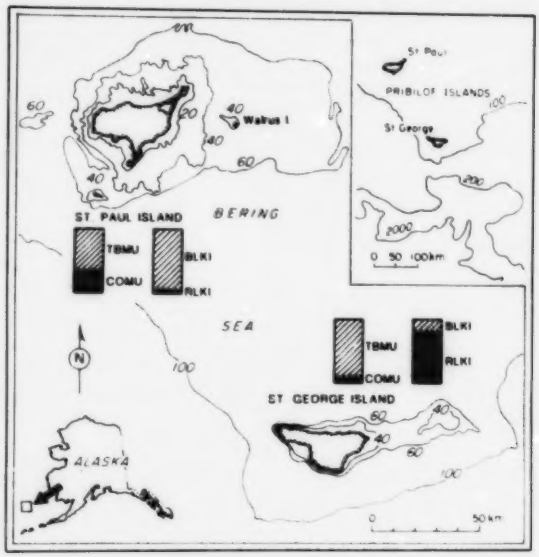
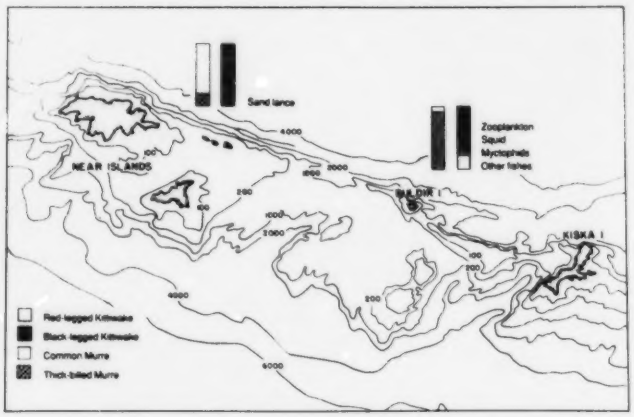


Figure 7
Relative numbers and principal prey of murres and kittiwakes in the western Aleutian Islands and the local bathymetry. Numerical data are from Byrd (1978, unpubl. data) and Byrd and Day (1986); dietary data are from AMS et al. (unpubl. data).



St. Lawrence Island and through western Bering Strait (Coachman et al. 1975; Sambrotto et al. 1984; Springer and Roseneau 1985; Springer et al. 1987, 1989; Grebmeier et al. 1988). This injection of an oceanic community into a shallow shelf environment gives seabirds access to a more diverse and abundant selection of prey, thus providing opportunities for more individuals of more species. In addition to the suite of piscivores on St. Lawrence Island, three species of planktivorous alcids, Least Auklets *Aethia pusilla*, Crested Auklets *A. cristatella*, and Parakeet Auklets *Cyclorrhynchus psittacula*, also nest in large numbers, compared with small numbers of Parakeet Auklets only in Norton Sound (Bédard 1969a; Steele and Drury 1977; Sowls et al. 1978).

Advection also extends the warm domain of Norton Sound northward into the otherwise cold environment of the eastern Chukchi Sea (Fig. 4). An associated community of boreal organisms, including sand lance, capelin, saffron cod, Common Murres, and Pigeon Guillemots *Cepphus columba*, enriches the Arctic fauna (e.g., Arctic cod, Thick-billed Murres, and Black Guillemots *C. grylle*) of the eastern Chukchi Sea (Springer et al. 1984).

4.2. Pribilof Islands

The Pribilof Islands are clustered near the shelf break in the southeastern Bering Sea (Fig. 1) and are surrounded by comparatively uniform oceanic waters. However, the islands are not equidistant from the shelf break, and the extent of shallow water around them is not the same. The different ratios of murres on the two largest islands, St. George Island and St. Paul Island (Fig. 6), are consistent with the general observation of an association of Common Murres with shallower shelf areas and, by implication, preferred prey. The greater relative and absolute numbers of Red-legged Kittiwakes on St. George Island also reflect its more oceanic nature. The relationship between relative numbers of seabirds on St. George Island and St. Paul Island and distance from the shelf break has been pointed out previously by Hunt et al. (1981a, 1981b) and Schneider and Hunt (1984).

4.3. Aleutian Islands

Buldir Island is a volcanic island rising steeply off the underlying Aleutian Arc and has little shallow water surrounding it (Fig. 7). The principal pelagic food web supporting seabirds nesting on Buldir Island is oceanic. There, the more numerous Thick-billed Murres feed primarily on squid (e.g., Gonatidae), as they do at sea southwest of the Aleutian Islands (Ogi 1980); Common Murres feed on a variety of fishes, including sand lance and young-of-year cods, and euphausiids; and both species of kittiwake feed on lanternfish. Black-legged Kittiwakes also supplement their diets considerably with oceanic zooplankton but uncommonly with sand lance or cods (AMS et al., unpubl. data).

The neighbouring Near Islands, in contrast, are surrounded by a much larger area of shallow water (Fig. 7) that apparently provides sufficient habitat for a typically coastal community to flourish. Most murres nesting on the Near Islands are Common Murres, which, along with Black-legged Kittiwakes, feed almost exclusively on sand lance. Red-legged Kittiwakes are absent. Red-faced Cormorants *Phalacrocorax urile* and Pelagic Cormorants *P. pelagicus* are abundant on the Near Islands, with a ratio of total cormorants:total murres of 2.5:1, compared with a ratio of just 0.018:1 on Buldir Island (Sowls et al. 1978; Byrd and Day 1986). Cormorants cannot dive to great depths, and on the Near Islands they feed heavily on sand lance (J. Piatt et al., unpubl. data).

If there is a strong relationship between seabird distribution and various marine food webs, it should be apparent in the Aleutian Islands, where, at the scale of the entire chain of islands, the marine environment is relatively uniform, but where the ratio of Common Murres to Thick-billed Murres varies greatly among the numerous colonies (Fig. 2). Assuming that particular prey are associated with particular habitats — for example, that sand lance are found in shallow, neritic environments — the extent of shallow water around an island should be a reasonable predictor of the ratio between the two species. And, indeed, there is a significant correlation between the relative number of Common and Thick-billed murres and the amount of shallow water surrounding the 11 Aleutian Islands having the largest murre populations (Fig. 8).

Figure 8
Relationship between water depth and the proportion of Common and Thick-billed murres on islands in the Aleutian Islands

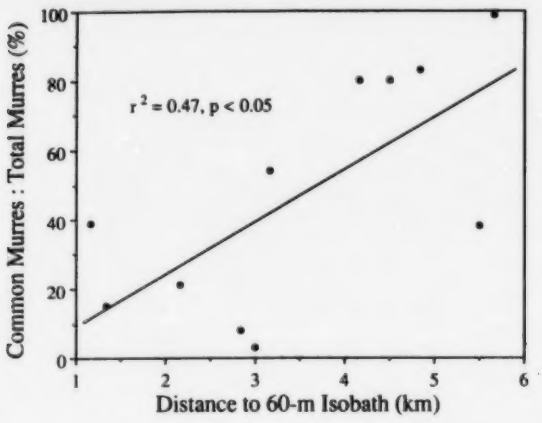


Figure 9
Sea surface temperature and estimates of Black-legged Kittiwake productivity at Cape Lisburne. An unusually great abundance of Arctic cod led to high productivity in 1983 in spite of cold water temperatures. From Springer et al. (1984, unpubl. data).

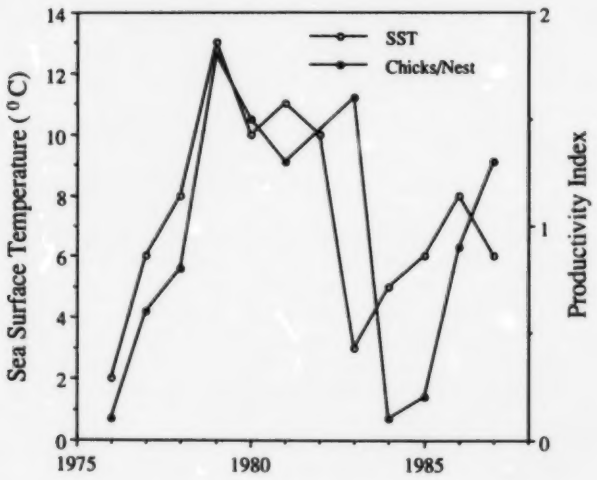
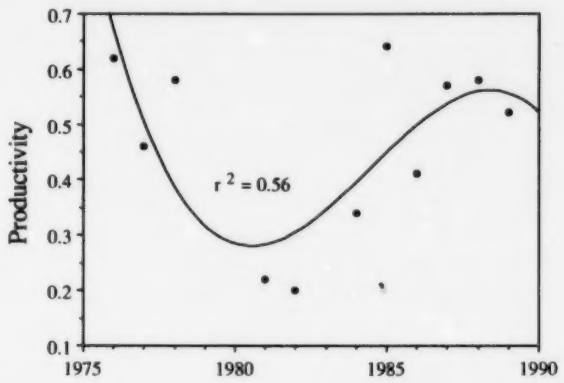
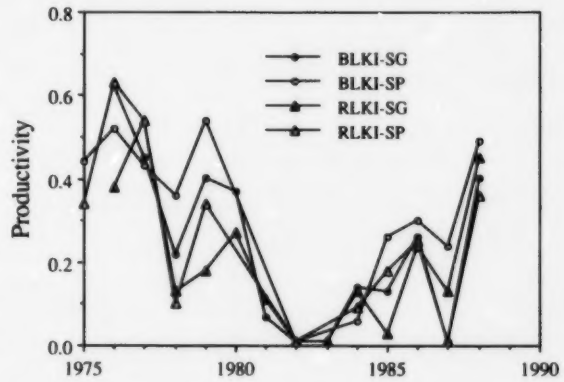


Figure 10
Estimates of murre and kittiwake productivity (chicks/nest) on the Pribilof Islands. BLKI and RLKI = Black-legged and Red-legged kittiwake, respectively; TBMU and COMU = Thick-billed and Common murre, respectively; SP and SG = St. Paul and St. George islands, respectively. From Hunt et al. (1981b), Lloyd (1985), Cra head and Oppenheim (1985), Johnson (1985), Byrd (1989, unpubl. data), and ... Sowls (unpubl. data).





5. Changes in populations of piscivorous species

Seabird distributions vary according to the type of marine environment and associated food webs, and seabird numbers and breeding biology are sensitive to fluctuations in prey abundance. Seabird studies therefore offer an unusual opportunity to evaluate effects of large-scale environmental changes on most of the principal pelagic food webs.

During the past 15 years, the reproductive success of murres and kittiwakes in Norton Sound and the eastern Chukchi Sea has been extremely variable between years (Springer et al. 1985, unpubl. data; Murphy et al. 1986, unpubl. data). In both regions, productivity has been poor in cold years and high in warm years (e.g., Fig. 9). The cycle in sea surface temperature appears to be linked to similar changes in the Bering Sea and Gulf of Alaska, where water temperatures have fluctuated in response to the lunar nodal tide (Royer 1989, unpubl. data) and the mean position of the Aleutian Low and resulting atmospheric circulation (Niebauer 1980). In the Bering Sea, however, the pattern of productivity has been just the opposite of that at the northern colonies (Fig. 10). That is, productivity was highest in the mid-1970s when ocean temperatures were coldest, declined as the environment warmed through the end of the decade, and has since increased in association with a recent cooling trend (Fig. 11). At all locations in years when productivity was low, few eggs were laid, many chicks died, or both, indicating that the underlying cause was inadequate availability of prey (i.e., fish).

Populations of kittiwakes and murres on the Pribilof Islands have declined since they were first censused in 1976 (Fig. 12). The only exception to this general pattern has been the relative stability of Common Murres on St. George Island. Unlike changes in productivity, which indicate fluctuating prey availability, the prolonged downward slide in numbers of kittiwakes and Thick-billed Murres on both islands and of Common Murres on St. Paul Island suggests a similar trend in prey abundance. Modeled estimates of the number of age-1 pollock in the southeastern Bering Sea indicate that recruitment has steadily declined since the early 1970s (Fig. 13). The slopes of the regression lines in Figures 12 and 13 are both between -3 and -4% per year.

Figure 11
Sea surface temperature in the southeastern Bering Sea. Compiled temperatures reported from a 5° square centred on 55°N × 170°W. From J. Namias (unpubl. data).

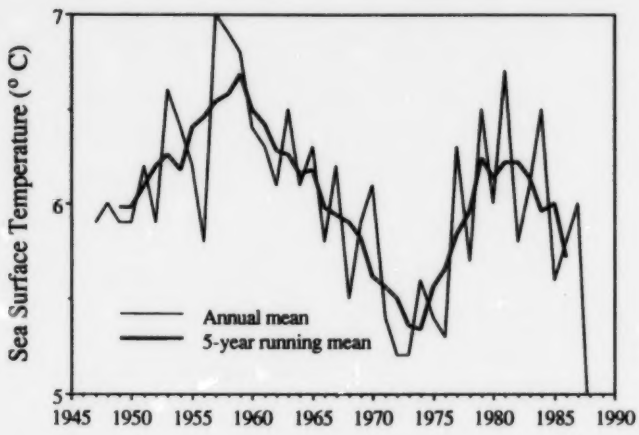
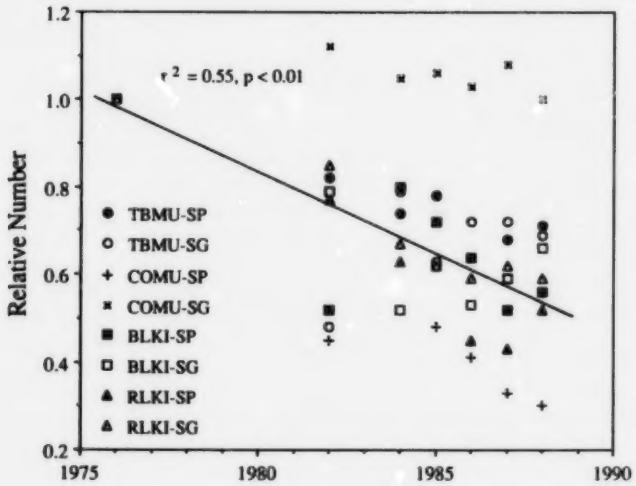


Figure 12
Trends in numbers of murres and kittiwakes on the Pribilof Islands. Abbreviations are as in Figure 10. From Hickey and Craighead (1977), Craighead and Oppenheim (1985), Johnson (1985), Byrd (1989, unpubl. data), and A. Sowls (unpubl. data).

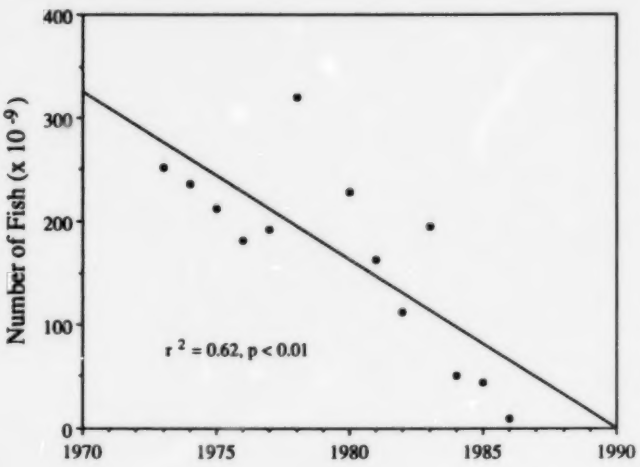


6. Relationships to avian planktivores

The pollock stock in the southeastern Bering Sea is one of the greatest consumers of zooplankton among a varied suite of planktivorous species. Combined, planktivores reputedly consume nearly the entire annual production of copepod biomass in the outer domain (Smith and Vidal 1984), where copepods constitute the bulk of the biomass of herbivores (Cooney 1981; Smith and Vidal 1984).

Least and Crested auklets are certainly the most conspicuous of the planktivores in the Bering Sea. During the breeding season, the dominant food of Least Auklets is copepods, primarily the large calanoids *Neocalanus plumchrus, N. cristatus,* and *Calanus marshallae,* whereas Crested Auklets consume many euphausiids in addition to copepods (Bédard 1969b; Hunt et al. 1981b; Springer and Roseneau 1985; Day and Byrd 1989). Both species of auklet are very abundant, particularly on some of the islands of the Aleutian chain and in the northern Bering Sea, where

Figure 13
Modeled numbers of age-1 pollock in the southeastern Bering Sea. The 1979 estimate, 7.34×10^{11}, is not shown and is not included in the regression. From T. Quinn (unpubl. data).

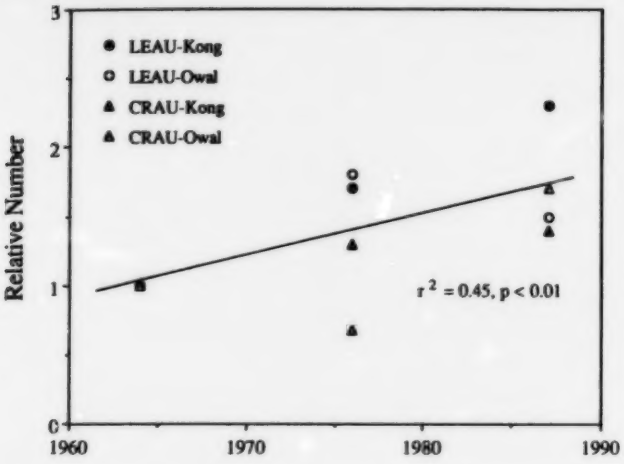


they number in the millions (Sowls et al. 1978). In comparison, there are about an order of magnitude fewer of each species on the Pribilof Islands and on St. Matthew and Hall islands, which lie near the centre of distribution of juvenile pollock.

If pollock are major competitors of auklets and other planktivores for copepods, then a change in the abundance of pollock as great as that in the southeastern Bering Sea should lead to measurable changes in auklet populations. In other circumstances, the breeding biology and apparent foraging efficiency of auklets can change in response to varying prey abundance over intervals of a few days to a year, suggesting that, in general, the birds are food-limited during the breeding season (Roseneau et al. 1985; Springer et al. 1986). If so, the nearly 50% decline in numbers of juvenile pollock could have been of significant benefit to them.

There are few population estimates for auklets, or indices that would detect numerical change, although limited data exist for the Pribilof Islands and St. Lawrence Island. Between 1976 and 1982 on the Pribilof Islands, Least Auklets apparently increased in number on both St. George Island and St. Paul Island, whereas Crested Auklets and Parakeet Auklets either increased or remained stable (Craighead and Oppenheim 1985). A third census in 1984 failed to indicate further gains (Johnson 1985), but the data are not entirely comparable with those from the two earlier years, and little time elapsed between the two censuses. Clearly, there is no indication of declining populations like those of the piscivores. Changes in auklet numbers on St. Lawrence Island are more compelling (Fig. 14). Although distant from the outer domain of the Bering Sea and the bulk of the pollock biomass, auklets on St. Lawrence Island and other colonies in the Bering Strait region are sustained primarily by oceanic zooplankton transported northward in the flow of water originating along the continental slope (Springer and Roseneau 1985; Springer et al. 1989). In the order of 5×10^{10} g of copepod biomass escaping pollock and other predators in the outer domain arrive daily during summer on the northern shelf. The apparent decline in pollock biomass since the mid-1970s should have led to a greater abundance of

Figure 14
Trend in numbers of auklets on western St. Lawrence Island. CRAU and LEAU = Crested and Least auklets, respectively; Kong and Owal = Kongkok Basin and Owalit Mountain colonies, respectively. From Bédard (1969b), Searing (1977), and Piatt et al. (1990).



zooplankton for other consumers, such as auklets, not just in the southeastern Bering Sea but on the northern shelf as well, and this could account for the increasing auklet populations on St. Lawrence Island.

7. Conclusions

The breeding distribution of seabirds in Alaska exhibits complex geographic patterns corresponding to the distribution of marine communities. These communities, in turn, are spatially organized by regional characteristics of marine environments (e.g., deep oceanic, shelf break, neritic, warm or cold). Although previous descriptions of seabird breeding distributions based solely on broad-scale features such as sea surface temperature are useful, they fail to account for underlying factors of prey distribution and "preferences" of seabirds for particular prey. In the Bering Sea, the marine environment often changes abruptly, with corresponding changes in communities and food webs that are easily detectable at higher trophic levels.

Most piscivorous seabirds in Alaska feed on only a few taxa of common forage fishes, particularly cods, sand lance, and capelin. The distribution of prey corresponds to the distribution of several species of seabirds: for example, Common Murres greatly outnumber Thick-billed Murres at all colonies in Alaska where the major prey is capelin or sand lance. An important exception to this generalization is in the oceanic domain, where zooplankton, lanternfishes, and squid support Red-legged Kittiwakes throughout their range as well as Black-legged Kittiwakes, Thick-billed Murres, and most other seabirds on Buldir Island and possibly similar oceanic islands in the Aleutian chain.

The close correspondence between murre and kittiwake productivity and sea surface temperature (but not always in the same way — cold water has been favourable for higher productivity on the Pribilof Islands, whereas warm water has been favourable in the northern Bering and eastern Chukchi seas) implicates fish abundance as an important intermediate element. Although the issue of changing prey abundance versus changing availability is unresolved, these insights into biophysical relationships in ecosystems are valuable in understanding patterns of variability and in predicting the consequences of future regional and global-scale factors, such as commercial fisheries and the greenhouse effect.

Long-term numerical changes in seabird populations in Alaska are not as well correlated with the physical environment as they are with other biological change. On the Pribilof Islands, where kittiwake productivity has fluctuated in phase with a cyclic trend in climate, kittiwake and murre numbers have declined steadily during this time. These changes closely match a drop in the estimated number of juvenile pollock in the southeastern Bering Sea. Such linear trends contrast with the cyclic nature of productivity and perhaps implicate causes other than variability in the physical environment. Other members of this pelagic community are fishermen, who in recent years have been harvesting 4–5 × 10^6 t of pollock annually in the Bering Sea (Dawson 1989; Wespestad 1989), or 35–42% of U.S. and Soviet estimates of the total exploitable biomass (Bulatov 1989; Wespestad 1989). The possible connection between this harvest and the changing condition of the stock is unknown. Elsewhere, however, fisheries have had extreme consequences on targeted stocks and consequently on seabird populations and entire marine communities (e.g., Schaefer 1970; May et al. 1979; Furness 1982; May 1984; Nettleship et al. 1984; Laws 1985).

Although information on planktivorous seabirds is scanty compared with that on the piscivores, it is consistent with the view that the pelagic food web of the Bering Sea is tightly coupled from primary producers to the higher trophic levels (Iverson et al. 1979; Smith and Vidal 1984; Springer et al. 1986; Walsh and McRoy 1986). If the stock of juvenile pollock has declined by half, as population models suggest, the potential gain in zooplankton biomass available to other consumers could account for increasing auklet numbers. Similar interactions have been invoked to explain changes in stocks of competing planktivores in the western North Atlantic (Vesin et al. 1981) and the Antarctic (May et al. 1979; Laws 1985).

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Appendix 1
Sources of data on the relative percentage of Common and Thick-billed murres (COMU:TBMU) and prey of murres, kittiwakes, and other piscivorous seabirds in the North Pacific and North Atlantic oceans

	Data source	
Region	**COMU:TBMU**	**Diet**
North Pacific Ocean	Tuck 1961 Vallee and Cannings 1983	Vermeer et al. 1987
Southeastern Alaska	Sowls et al. 1978	
Forrester I.	DeGange et al. 1977	Heath 1915 DeGange et al. 1977
St. Lazaria I.	Nelson et al. 1987	
Sealion Is.	AMS and G.B. van Vliet, unpubl. data	AMS and G.B. van Vliet, unpubl. data
Prince William Sound	Isleib and Kessel 1973 Sowls et al. 1978	Baird and Gould 1986
Gulf of Alaska	Sowls et al. 1978	Baird and Gould 1986 Sanger 1987 Sanger and Hatch 1987
Middleton I.	Rausch 1958 Hatch 1983	
Barren Is.	Bailey 1976	
Kenai Peninsula	Bailey 1977	
Sandman Reefs	Bailey and Faust 1980	
Alaska Peninsula	Bailey and Faust 1984	
Shumagin Is.	Bailey 1978	
Simidi Is.		Hatch 1984
Aleutian Islands	Sowls et al. 1978	
Bogoslaf I.	Byrd et al. 1980	
Fire I.	Byrd et al. 1980	
Kagamil I.	Bailey and Trapp 1986	
Chagulak I.	Bailey and Trapp 1986	
Amukta I.	Bailey and Trapp 1986	
Seguam I.	Bailey and Trapp 1986	
Adak I.		G.V. Byrd et al., unpubl. data
Bobrof I.	Day et al. 1978	
Amchitka I.		Williamson et al. 1972
Gareloi I.	Day et al. 1978	
Ulak-Amatignak Is.	Day et al. 1978	
Semisopochnoi I.	Day et al. 1978	
Buldir I.	Byrd and Day 1986	AMS et al., unpubl. data
Near Is.	G.V. Byrd, unpubl. data	AMS et al., unpubl. data
Sea of Okhotsk		Ogi and Tsujita 1977
W Kamchatka Peninsula	Vyatkin 1986	
Penzhin Inlet	Vyatkin 1986	
Sakhalin I.	Nechaev 1986	Mikhtaryantz 1986
W Bering Sea	Golovkin 1984	
E Kamchatka Peninsula	Vyatkin 1986	
Karaginsky I.	Vyatkin 1986	
Olyutorskoe Shore	Vyatkin 1986	
E Bering Sea	Sowls et al. 1978	
Cape Peirce	Peterson and Sigman 1977	Lloyd 1985
Bristol Bay		Ogi and Tsujita 1973
Pribilof Is.	Hickey and Craighead 1977	Hunt et al. 1981a
St. Matthew-Hall Is.	D.G. Roseneau et al., unpubl. data	Springer et al. 1986 Murphy et al. 1987
N Bering Sea	Sowls et al. 1978 Golovkin 1984	Ogi and Hamanaka 1982 Ogi et al. 1985
St. Lawrence I.	D.G. Roseneau and AMS, unpubl. data	Springer et al. 1987
Little Diomede I.	Biderman and Drury 1978	
King I.	Drury and Steele 1977	
Norton Sound	Drury 1977	Springer et al. 1987
W Chukchi Sea	Golovkin 1984 Kondratiev 1986	A.Y. Kondratiev, unpubl. data
E Chukchi Sea	Sowls et al. 1978	
Cape Lisburne	AMS et al., unpubl. data	Springer et al. 1984
Cape Thompson	Swartz 1966 D.G. Roseneau et al., unpubl. data	Swartz 1966 Springer et al. 1984
Kotzebue Sound	Nelson and Sowls 1985	
Beaufort Sea	Johnson and Ward 1985	

Appendix 1 *(cont'd)*
Sources of data on the relative percentage of Common and Thick-billed murres (COMU:TBMU) and prey of murres, kittiwakes, and other piscivorous seabirds in the North Pacific and North Atlantic oceans

	Data source	
Region	**COMU:TBMU**	**Diet**
North Atlantic Ocean	Tuck 1961 Nettleship and Evans 1985	Tuck 1961 Bradstreet and Brown 1985
British Isles		Pearson 1968
Norway		Myrberget 1962, *in* Lidd 1980 Furness and Barrett 1985
Barents Sea		
Murmansk		Belopol'skii 1957
Novaya Zemlya		Uspenski 1956 Krasovsky 1937, *in* Belopol'skii 1957
Labrador Sea		
Newfoundland	Cairns et al. 1989	Brown and Nettleship 1984 Piatt 1987
Akpatok I.		Tuck and Squires 1955
Lancaster Sound		
Barrow Strait		Bradstreet 1980
Prince Leopold I.		Gaston and Nettleship 1981

Marine birds and climatic warming in the northwest Atlantic

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Abstract

Current climate models predict a significant warming of the global atmosphere in the near future. This "greenhouse effect" will be due to the trapping of infrared radiation inside an increasing outer layer of carbon dioxide (CO_2), produced mainly by the burning of fossil fuels. The models predict that, by about AD 2050, the thickness of the CO_2 layer will double, leading to an atmospheric temperature increase of between approximately 1.0 and 4.5°C. Thermal expansion of the water column and meltwater from the ice caps are predicted to cause a global increase in sea level in the order of 1.0 m by about AD 2050, modified in the longer term by vertical, isostatic movements of the shorelines.

This paper speculates about the effects of these changes on some eastern Canadian seabirds, based on their ecology today. Northerly shifts in ranges are likely off Nova Scotia and Newfoundland. These will probably be due as much to shifts in the ranges of prey species as to the direct effects of warming on the birds themselves. The melting of the high-Arctic pack ice should create new polynyas and similar feeding habitats for Dovekies *Alle alle*. The increase in sea level, added to storm surges and the tides, will probably eliminate important low-lying breeding sites, such as Funk and Sable islands, as well as the mudflats at the head of the Bay of Fundy, used by migrant shorebirds in the fall.

Résumé

Les modèles climatiques actuels prévoient un réchauffement important de l'atmosphère à l'échelle de la planète dans un avenir prochain. Le phénomène, appelé communément «effet de serre», est dû à l'emprisonnement des rayons infrarouges à l'intérieur de la couche externe de dioxyde de carbone (CO_2) qui s'épaissit de plus en plus sous l'action principalement de la combustion des combustibles fossiles. D'après les modèles, l'épaisseur de la couche de CO_2 doublera d'ici l'an 2050 approximativement, entraînant une augmentation de la température de l'ordre de 1,0 à 4,5 °C. L'expansion des colonnes d'eau et la fonte des calottes glaciaires qui accompagneront ce réchauffement devraient se traduire par une élévation générale du niveau de la mer d'à peu près 1,0 m d'ici l'an 2050 environ, avec à plus long terme des mouvements isostatiques, verticaux, des côtes.

L'auteur fait des conjectures sur les conséquences de ces changements pour certains oiseaux de mer de l'est du Canada, compte tenu de leurs caractéristiques écologiques actuelles. Un déplacement vers le nord de leurs aires de répartition est probable au large de la Nouvelle-Écosse et de Terre-Neuve. Ce déplacement devrait être autant la résultante du déplacement des organismes dont ils se nourrissent qu'un effet direct du réchauffement. La fonte de la banquise dans l'Extrême-Arctique devrait créer de nouvelles polynies et d'autres habitats similaires, propices à l'alimentation des Mergules nains *Alle alle*. La hausse du niveau de la mer, s'ajoutant aux vagues de tempête et aux marées, entraînera probablement la perte d'importants lieux de nidification situés sur des terres basses, comme l'île Funk et l'île de Sable, de même que la disparition des vasières du fond de la baie de Fundy, qui sont utilisées par des oiseaux de rivage au moment de leur migration à l'automne.

1. Introduction

Most discussions of the "greenhouse effect" stress the warming up of the atmosphere and the implications this has for us as terrestrial animals: short winters and summer droughts, for instance. Many of these changes will also have indirect oceanographic consequences: for example, droughts will reduce river outflows and thus the transfer of terrestrial nutrients to marine food webs. However, the emphasis in this speculative review will be on the other side of the oceanic–atmospheric linkage: the direct, short- to medium-term ways in which warmer oceans may be expected to affect the breeding and feeding ecology of marine birds.

Atlantic Canada has a long coastline and a wide and highly productive continental shelf. It also has very large breeding populations of seabirds. There are some 5 million pairs of Leach's Storm-Petrels *Oceanodroma leucorhoa* and 1.5 million of the other principal colonial species, mainly in Newfoundland (Brown and Nettleship 1984a; Cairns et al. 1986). However, these are probably outnumbered by migrants at all times of year. In winter, the largest contribution comes from the seabird colonies in west Greenland and Arctic Canada: >7.0 and 1.75 million pairs, respectively (Brown and Nettleship 1984a; Evans 1984). In summer, there are >5 million Greater Shearwaters *Puffinus gravis* and large numbers of Sooty Shearwaters *P. griseus* and Wilson's Storm-Petrels *Oceanites oceanicus* "wintering" here from colonies in the sub-Antarctic, as well as nonbreeding Northern Fulmars *Fulmarus glacialis* and Black-legged Kittiwakes *Rissa tridactyla* from Europe and the Arctic (e.g., Palmer 1962; Cramp 1977, 1983). These

rough estimates take no account of the Arctic waterfowl and shorebirds that stage through or winter in coastal habitats in Atlantic Canada (e.g., Palmer 1976; Hicklin and Smith 1984; Mercier 1985; Brown and Gaskin 1988). Clearly, "our" marine birds will be affected by distant environmental events. Conversely, changes in Atlantic Canada may become apparent only at very distant colonies.

Up to now, the principal risks to seabird populations have come directly from human destruction of feeding and breeding habitats. The immediate, new concern is with the large-scale changes that may follow climatic warming. The potential scale of the "greenhouse effect" is so enormous that it is hard to grasp its implications, except perhaps by speculating about a familiar corner of the environment. This paper makes no attempt to review all the possibilities for change in the marine environment off eastern Canada. Instead, it presents some speculative scenarios for change, as they might affect our seabird, waterfowl, and shorebird populations.

2. Oceanographic and climatological background

The physical and biological oceanography of the northwest Atlantic is determined by circulation patterns, which in turn depend on the water movements set up by wind stresses, pressure gradients, and the Earth's rotation, within limits set by the coastlines (e.g., Brown 1986) (Fig. 1). The warm Gulf Stream (or North Atlantic Drift) is the northwestern sector of the clockwise gyre that dominates circulation in the North Atlantic. It flows up the American coast to Cape Hatteras and then diagonally across to Europe. Warm branches go up to west Greenland and the Norwegian Sea, but the main flow turns south, and then west, to complete the gyre. The other major feature off Atlantic Canada is the cold Labrador Current, flowing out of Baffin Bay and down the coast of Labrador to the Grand Banks, where it is turned east by the Gulf Stream. These two currents and their associated wind systems determine the climate, ice cover, storm tracks, and distributions of marine biological communities off eastern Canada.

Climatic warming will presumably change atmospheric circulation patterns to some extent, and therefore the paths of these currents (e.g., Evans and Nettleship 1985), although the positions of the land masses will probably restrict the geographical scope of such shifts. More generally, there will be an increase in the mean temperature of the Earth's atmosphere. Increasing concentrations of CO_2 and other gases trap the sun's infrared rays and prevent them from radiating out again — just as solar heat is trapped inside a greenhouse by a layer of glass. Much of the CO_2 comes from burning fossil fuels; its concentration in the atmosphere is expected to double over the next 50–75 years. Present predictions suggest that this will raise the mean atmospheric temperature by between 1.0 and 4.5°C by AD 2050 — but by considerably more in the polar regions (e.g., Kerr 1988; Ramanathan 1988; Tangley 1988; Lewis 1989).

The sea level will rise — at first by the thermal expansion of the water column, and then with water from the melting ice caps and permafrost. The predicted rise will be at least 0.2 m, perhaps 1.4 m, by AD 2050, although this may be an underestimate (Tangley 1988; Lewis 1989). It is possible that the process has already begun (Peltier and Tushingham 1989). Later events are difficult to forecast. Recent analyses of satellite data suggest a positive feedback loop between sea surface temperatures and the water vapour in the atmosphere that will intensify the heating of the "greenhouse" (Raval and Ramanathan 1989; Gribbin 1990). On the other hand, computer simulations of the thawing of the ice caps suggest a feedback in the opposite direction, giving an increase of only 0.3 m during that period, or possibly no change at all (Meier 1990). Indeed, precipitation falling as snow may even *increase* the size of the ice caps. Prediction is further complicated by the fact that the "greenhouse" warming is superimposed on a global climate that, in the long term, has been cooling down "naturally" since the 1950s (Berry 1981).

However, marine scenarios have emphasized the effects of an eventual rise in sea level, and this is the point of greatest concern to marine ornithologists. For present purposes, we will assume a rise in the order of 1.0 m by AD 2050. This does not mean that all coastlines will be submerged to that depth. Studies of the last deglaciation, between 18 000 and 6000 BP, show that Greenland and Ellesmere Island, freed of the weight of much of their ice caps, rose and are still rising (e.g., Walcott 1972). Meanwhile, on the other side of the geological plate, the coasts south of Nova Scotia sink, teeter-totter fashion. These vertical, isostatic changes will undoubtedly continue as the "greenhouse effect" warms the atmosphere, giving apparent changes in sea level both greater and less than the suggested mean of 1.0 m.

There may also be local variations in the rates at which the ice will melt. I suggest that the warming of eastern Canada will be buffered to some extent by the fact that Baffin Bay is nearly an enclosed sea, with only one major opening, and with one of its sides formed by the Greenland Ice Cap (e.g., Dunbar 1951; Anon. 1988). The relatively thin, permanent pack ice in the Bay and in the Arctic Ocean will probably melt fairly quickly once the atmosphere warms up. However, the Ice Cap has an area of 1.8 million square kilometres and an average thickness of 1.5 km, covering 85% of the island. This should take some time to disappear. The position of the Labrador Current, the only major outflow from the Bay, is channeled down towards Newfoundland by the mountainous coastlines of Baffin Bay and Labrador, and this is unlikely to change. So, by extension, the present cooling influence of Baffin Bay on Atlantic Canada will probably persist for a while.

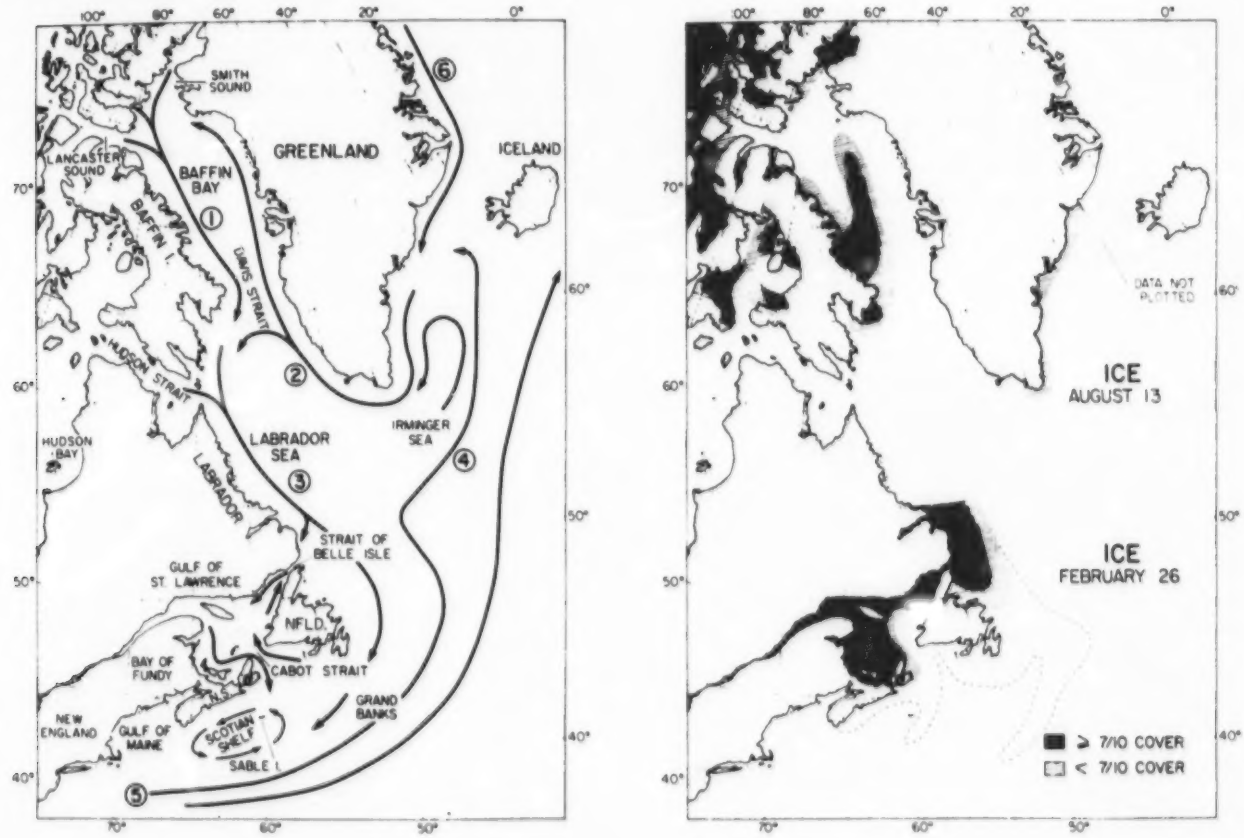
3. Marine birds: scenarios for change

3.1. Boreal and low-Arctic seabirds

On these assumptions, it is likely that the northern distribution limits of eastern Canadian seabirds will remain relatively unchanged at first, but the southern limits will gradually retreat, as the subtropical zone warms up and expands northwards. It will be interesting to watch the breeding ranges of the boreal/low-Arctic Common Murre *Uria aalge* and the low-/high-Arctic Thick-billed Murre *U. lomvia* (Nettleship and Evans 1985). Today, in the western Atlantic, their principal overlap is in southeast Labrador. A northward expansion of Common Murres should be easy to monitor, because the sites and sizes of both species' colonies in eastern Canada are fairly well known.

Farther south, we should expect similar northward shifts in the distributions of large shearwaters. Today, in July–August, Cory's Shearwater *Calonectris diomedea* is most common close to the Gulf Stream, especially on southern Georges Bank; Greater Shearwaters are abundant from Georges up to southeast Labrador (Brown 1977;

Figure 1
(Left) The principal current systems in the northwest Atlantic and eastern Canadian Arctic: 1 — Baffin Land Current; 2 — West Greenland Current; 3 — Labrador Current; 4 — North Atlantic Drift; 5 — Gulf Stream; 6 — East Greenland Current. (Right) Minimum and maximum pack-ice cover, ca. 1970. The map shows the average southern extent of pack ice on 13 August (minimum) and 26 February (maximum). The broken line marks the approximate limit of drift ice in April–May (from Brown 1986).



Powers and Brown 1987). Both are nonbreeding migrants, presumably free to follow changes in prey distributions. However, even relative changes in their distributions will be hard to measure, because pelagic seabird surveys are very imprecise indices. Cory's Shearwaters were unusually common off southern Nova Scotia in 1988 (Brown 1989), and it is tempting to link this to the unusually warm summer that year and to climatic warming in general. However, we do not know how widely the birds' ranges fluctuate, even in "normal" summers. If Cory's Shearwater were to become the dominant shearwater on the Scotian Shelf for several summers in a row, this would indeed suggest a significant, northerly expansion in range. It will be hard to detect anything less obvious than this.

Changes in range need not indicate the birds' direct response to increasing air and water temperatures. They may be responding to temperature-induced changes in the distributions of their principal prey. Capelin *Mallotus villosus* and Arctic cod *Boreogadus saida* are important prey for fish-eating alcids and other seabirds off Newfoundland and Labrador (e.g., Brown and Nettleship 1984b; Bradstreet and Brown 1985). Both are common in the cold Labrador Current but scarce or absent in the relatively warmer waters of the Scotian Shelf and the southern Gulf of St. Lawrence (Scott and Scott 1988). Newfoundland capelin spawn at average water temperatures of 6–7°C, ranging between 2.8 and 10.8°C, depending on the area and season. Adult Arctic cod are most common in waters of 0–4.0°C. Both species will probably retreat northwards as water temperatures rise. The cod might be replaced by warm-water gadoids such as haddock *Melanogrammus aeglefinus*, which has a preferred summer range of 4–8°C.

However, seabirds will require more than the mere presence of, say, capelin off northern Labrador; they will need them in schools large enough for economical foraging. Alcids are notoriously conservative in their choice of nest sites; new colonies are explored by immature birds (e.g., Kress 1982), so this will impose a further time lag. It is likely that the fish will shift their ranges before the murres begin to do so.

3.2. High-Arctic seabirds

The southern limits of many winter visitors from the Arctic will probably withdraw northwards as the Atlantic warms up. Ivory Gulls *Pagophila eburnea* are closely associated with the pack ice off Newfoundland in spring, scavenging on the herds of harp seals *Phoca groenlandica* and hood seals *Cystophora cristata* pupping

on the ice (Banfield 1974; Cramp 1983; Godfrey 1986). These gulls and the seals will probably be among the first to retreat.

When the northern limits of seabird breeding ranges begin to shift, it may well be a positive response to *improved* conditions, as opposed to a passive "squeeze" forced on the birds by warmer temperatures farther south. In the eastern North American Arctic, for example, the major Thick-billed Murre colonies are on coasts where the sea either never freezes offshore or breaks up early in the spring: southwest Greenland, Hudson Strait, and the North Water polynya at the top of Baffin Bay (Evans 1984; Nettleship and Evans 1985). The largest colonies of Dovekies *Alle alle* are all at the northern edges of such open areas: mainly in northwest Greenland, but also in Scoresby-Sund, Spitsbergen, and Franz Josef Land (Nettleship and Evans 1985: Table 2.3). These alcids, and seabirds in general, will benefit from the warming trend in several ways. The retreating pack ice will open up more feeding areas in spring. It will also give the phytoplankton an earlier exposure to the long daylight, and this, in turn, will give zooplankton an earlier start in the short Arctic summer. The early melting of snow cover will expose more slopes to breeding Dovekies. This species, with at least 7 million pairs breeding beside the North Water, is already the most common seabird in the Arctic. It will probably expand its numbers and range northwards into north Greenland and the Canadian high Arctic as the pack ice disappears.

3.3. Phalaropes

Red Phalaropes *Phalaropus fulicarius* and Red-necked Phalaropes *P. lobatus* are seabirds for only part of the year: they breed on the Arctic tundra, often a long way inland (Cramp 1983). Some of their breeding areas will be lost if the thawing of the permafrost leads to extensive flooding in low-lying areas. On the other hand, the floods will provide extensive new nurseries for the aquatic insect larvae that are the phalaropes' principal food in summer. However, that will be only a short-term benefit. The insects will die off as soon as the sea level rises enough to taint the freshwater pools.

Outside the breeding season, phalaropes feed on marine zooplankton in areas where it is concentrated at the surface by upwellings, "fronts," and similar oceanographic phenomena (Cramp 1983; Mercier 1985; Brown and Gaskin 1988). Very large flocks — perhaps all the birds in the eastern Canadian Arctic — migrate through the outer Bay of Fundy in the fall, feeding on swarms of copepods "pumped" to the surface by the strong tidal streams. Greenberg (1986) predicted that an extra 1.0 m in the water column offshore would result in a 1.7% increase in tidal range in the inner Gulf of Maine, including Fundy. How will this affect the efficiency of the "pump," and what else will it do to the Fundy tides in general?

After their stopover, the phalaropes fly south to winter in the cool, highly productive upwellings off Peru and West Africa. However, the Peru upwelling fails every few years and is temporarily replaced by an influx of warm water. This is the "El Niño" phenomenon, in which large numbers of marine organisms, including seabirds, die off (e.g., Murphy 1936). Will the frequency or, more probably, the intensity of "El Niño" events increase as the climate warms up?

3.4. Coastal breeding and feeding sites

Rising sea levels will have direct effects on several types of marine bird habitat. Most of the big seabird colonies in Newfoundland and the Arctic are on high, steep cliffs and should be safe. But Funk Island, Nfld., with about 0.5 million pairs of Common Murres, 6000 Northern Gannets *Morus bassanus*, and several other breeding seabirds, is a low rock only 15 m high (Brown and Nettleship 1984a; Nettleship and Evans 1985; Anon. 1986; Cairns et al. 1986). The colony will not be completely submerged, but the increase in sea level will make it more vulnerable to storm surges. The coastal sandbars in Nova Scotia and the Gulf of St. Lawrence, on which the endangered Piping Plover *Charadrius melodus* and many terns breed, will also be at risk, along with the dunes that are the principal habitat of Sharp-tailed Sparrows *Ammodramus caudacutus* (e.g., Godfrey 1986; Tufts 1986). The probable erosion and submergence of Sable Island (24 m: Anon. 1985), an isolated sand dune 180 km east of Nova Scotia, will eliminate a breeding site for the threatened Roseate Tern *Sterna dougallii*. The rare Ipswich Sparrow *Passerculus sandwichensis princeps*, breeding only on Sable and a few sites on the mainland coast, will almost certainly become extinct. The large colony of grey seals *Halichoerus grypus* will probably be lost, but the harbour seals *Phoca vitulina* on the island, with more amphibious pupping habits, will remain (e.g., Banfield 1974).

The saltwater and freshwater marshes at the head of the Bay of Fundy are important breeding and feeding areas for "puddle ducks" — and not just the ubiquitous American Black Duck *Anas rubripes* of Atlantic Canada. Northern Shoveler *Anas clypeata*, Gadwall *A. strepera*, American Wigeon *A. americana*, and other typically western species are at the eastern edge of their ranges (Palmer 1976; Godfrey 1986; Tufts 1986). These low-lying areas will be vulnerable to any increase in the height of the strong Fundy tidal streams and to storm-induced surges (e.g., Walcott 1975).

In the adjacent part of the Bay, these tides have created highly productive mudflats, exposed twice a day, where the abundant amphipod *Corophium volutator* is exploited by very large numbers of migrant shorebirds. The Semipalmated Sandpiper *Calidris pusilla*, with flocks of >1 million birds, is the most common species (Hicklin and Smith 1984). This is a critical feeding stopover in July-August, when the birds move from the Arctic to their winter quarters in Guyana and Surinam. Inner Fundy is as crucial to these migrants as Outer Fundy is to the phalaropes (see above). A sea level rise of 1.0 m, magnified by the increase in tidal range (Greenberg 1986), will permanently submerge much of the existing intertidal zone, although new mudflats will presumably form inshore above the newly formed beaches.

In spring, the sandpipers' stopover is in Delaware Bay, about 35°N, where they feed on the abundant eggs of horseshoe crabs *Limulus polyphemus*. This spawning may be disrupted by changes in tidal range. It is also possible that warmer sea temperatures will put the crabs' spawning cycle out of phase with the birds' migration patterns (Pain 1988).

4. Discussion

It is hard to know how much to believe of these scenarios. In one sense, they are only as good as the latest computer climate simulations, which change continually. Perhaps their main value is to alert marine ornithologists to the kinds of changes we should expect and be prepared to study. Here are three more unpredictables to round off this essay in speculation.

First, it has been a basic assumption, here as in other "greenhouse" predictions, that the warming will be relatively gradual, allowing the biota a little time to adapt to it. However, the history of the deglaciation after the last Ice Age shows that this need not be so. Sea levels have been reconstructed from core samples bored in coral reefs (e.g., Fairbanks 1989; Shackleton 1989). These show an overall rise of about 121 m over 17 000 years, but this was very much a stop-and-go affair. There were two very rapid, warming increases, but, at other times, glaciation apparently started all over again. What will happen to our predictions if the "greenhouse" deglaciation also has irregular, rapidly changing rhythms?

Next, these speculations have all dealt with the effects of warming on the birds' marine environments. The physiological stresses on the birds themselves are harder to assess. Healthy seabirds have little difficulty in coping with extreme cold; they are insulated by their feathers and by subcutaneous fat. Black Guillemots *Cepphus grylle*, for example, winter as far north as 80°N (Brown 1985). But, because of this, they may have difficulty in keeping cool. In Atlantic Canada even today, young Northern Gannets find it harder to cope with heat stress than with cold (Montevecchi and Vaughan 1989). Warm temperatures may therefore set southern limits to seabird distributions that need have nothing to do with the availability of suitable prey or breeding sites.

Finally, we must not underestimate the unpredictability of the animals themselves, however well we think we know them. The unexpected versatility of introduced species has shown this many times. But there is also an apt historical scenario that makes this point for the northwest Atlantic at the end of the last Ice Age (Pitt 1958; Rutter 1988; Scott and Scott 1988). Capelin, central to marine food webs off Newfoundland, are fish that normally spawn on gravel beaches in the intertidal zone. This was a very extensive habitat in 18 000 BP, when the southern tip of the Grand Bank was above the surface. But a Neolithic biologist watching the sea level rise might well have predicted that this capelin stock, and the predators feeding on it, would disappear as soon as the beaches were submerged and the Gulf Stream moved north to warm the oceanic climate. Yet capelin still spawn there, 375 km offshore, on "beaches" 50 m underwater, and in numbers that support large populations of moulting Greater Shearwaters, lactating baleen whales, and a major ground fishery (e.g., Brown 1988, pers. obs.).

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